THE RELATIVE ABUNDANCE AND DISTRIBUTION OF PENAEID SHRIMP LARVAE OFF THE MISSISSIPPI COAST

by

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INTRODUCTION

Penaeid shrimp go through a complicated metamorphic life cycle involving a change in their habitat during the course of development. Adults inhabit and spawn in highly saline offshore waters, the larvae are planktonic and the postlarvae migrate into low saline coastal bays for their survival and growth. Spawning cycles of several species in the Gulf of Mexico have been studied chiefly by collecting the mature adults. A considerable volume of work has been done on the biology of the postlarvae, but information on the planktonic larvae is scanty. Assessment of reproductive cycles of marine animals based on the larval abundance is one of the several methods employed by biologists (Giese 1959). This method is particularly applicable to animals such as penaeid shrimp, which are benthonic.

The literature on the development and various other aspects of the biology of the penaeid shrimp is becoming voluminous. Many investigations have considered the spawning seasons, especially of commercially important species. Since Müller (1864) showed that the penaeid egg hatches into a nauplius, a series of investigations have traced the development of several species, especially those by Gurney (1924, 1927, 1942, 1943), Hudinaga (1942), Menon (1951), Heldt (1938, 1954, 1955), Heegaard (1966) from various parts of the world; Pearson (1939), Heegaard (1953), Dobkin (1961), Renfro and Cook (1963), and Cook and Murphy (1965a), from the Gulf of Mexico. Cook (1966) worked out a generic key for the identification of larvae to the generic level.

The commercial importance of penaeid shrimp evoked a great interest in the study of their biology, and a considerable amount of information has accumulated as reviewed by Williams (1965) and Lindner and Cook (1967). A useful bibliography has been prepared by Chin and Allen (1959). The first to un-

derstand that the penaeid shrimp spawn in the littoral water was Viosca (1920) who stated that *Penaeus setiferus* (Linn.), a synonym of *P. fluviatilis* Say when applied to North American white shrimp, spawns in the Gulf, chiefly on the evidence that mature shrimp are found only in outside waters. The young are said to live in the plankton of the Gulf until a size of 1¼ inch[1] is reached. Now it has been well established that this generalization is true. However, the size at which the postlarvae enter the bays is 7 mm (Weymouth, Lindner, and Anderson 1933). Actually some postlarvae are 12 mm or slightly more at this stage. After spending a variable period in the plankton, larvae metamorphose into postlarvae and migrate into coastal inland waters. They grow very rapidly in the low saline environment. This was first discovered by Viosca (1920), and was rediscovered by Gunter (1950), after it was forgotten or ignored for 30 years. Gunter states that the young white shrimp grow 25 to 45 mm per month during warmer months. Williams (1955a) has confirmed this.

The most thoroughly investigated species is the white shrimp, *Penaeus fluviatilis* Say, which has been studied in detail by Weymouth *et al.* (1933), Pearson (1939), Anderson, King and Lindner (1949), Gunter (1950), Anderson (1955), Lindner and Anderson (1956), Christmas and Gunter (1967) and Lindner and Cook (1967). According to these authors, the white shrimp spawn mainly from spring through late fall with variable peaks in different geographical areas. The brown shrimp, *P. aztecus* Ives, is believed to spawn through an extended period with little variation along its range (Gunter 1950), Kutkuhn 1962, and Williams 1965). The peak spawning seasons of this species are March-April and September-October. The pink shrimp, *P. duorarum* Burkenroad, has been studied extensively on the Florida coast by Eldred *et al.* (1961, 1965), Idyll, Jones and Dimitriou (1962) and Iversen and Idyll (1960). It breeds from spring to late summer or late fall according to these authors, but Roessler, Jones and Munro (1967) believe that it spawns year round.

The other species have not received as much attention as the species of *Penaeus*. From the available information (Pearson 1939, and Eldred *et al.* 1965), it appears that *Trachypeneus* spp. breed from February to November; *Parapenaeus longirostris* (Lucas) from April to June or October; *Sicyonia* spp. from January to December with summer peaks; and *Solenocera* spp. from February to June or November. These conclusions have been based on studies made on the larvae or the adults at a particular depth or a few depths.

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[1]Editorial note. Viosca always maintained that his measurements were in cm and they were botched by printers.

Most of the species of penaeid shrimp in the Gulf of Mexico appear to breed when the temperature rises in spring and exhibit peaks in spring or summer and in fall. The paramount importance of temperature in controlling the breeding and distribution of marine animals has been emphasized by Orton (1920), Thorson (1946, 1950), Ekman (1953), Gunter (1957), Johnson (1957) and Radovich (1961). Orton's rule states that, "most marine animals under normal conditions begin to breed either at a definite temperature, which is a physiological constant for the species, or at a definite temperature change, namely, at either the maximum or the minimum temperature of the locality." Rising temperatures induce gonadal development in most temperate organisms, and actual spawning takes place when a certain temperature, which varies with different species, is reached (Gunter 1957).

While the occurrence of mature adults and of larvae sheds light on the reproductive cycles of shrimp, the abundance of postlarvae in the backwaters offers corroborative evidence. Contributions on this phase of the shrimp life history have been made by Williams (1955 a,b, 1959 and 1969), Gunter (1961 a,b), Renfro (1960, 1961), Loesch (1965), Christmas, Gunter and Musgrave (1966) and Baxter and Renfro (1967). These authors have discussed the incidence of postlarvae in the bays, which occur in two or three waves, and these waves of abundance correlate with the spawning seasons.

It can be seen that the important larval phase of the life cycle has not received much attention. The occurrence of larvae is a definite sign of spawning activity, especially of the benthonic animals or sessile animals such as oysters (Korringa 1957). The first study purely on larval distribution was made by Eldred *et al.* (1965) who discussed trends in abundance in west Florida waters up to 37.8 m deep, and showed that spawning peaks varied at different depths for various species of six genera. Temple and Fischer (1965) studied the vertical distribution of the four larval stages and elucidated their vertical stratification and diurnal changes. The same authors discussed the relative abundance and distribution of *Penaeus* larvae off Galveston (Temple and Fischer 1967), and showed that the breeding season tended to be more protracted progressively with depth, and that the peak spawning season differed at different depths.

Thus, the information on the distribution of larvae of various commercial penaeids of the South Atlantic and Gulf of Mexico is limited to these three studies. Sampling at one water depth and at one particular level in the water column will not yield accurate information on the previous spawning activity of benthonic animals. Also, the distribution of larvae in relation to season, temperature, salinity and depth is of fundamental biological interest.

The objectives of the present investigation are: (a) to delineate spawning seasons and the areas of as many species as possible based on larval abundance; (b) to study the spatial and seasonal distribution of penaeid larvae in relation to depth, temperature, salinity and seasons, which will indicate the movements of the spawners; (c) to inquire whether any correlation exists between occurrence of larvae and of adults in any area; (d) to examine the relationship between *Penaeus* postlarval abundance in the Mississippi Sound and larval and postlarval occurrence in the open sea; and (e) to study the vertical seasonal distribution of different stages, and to find out whether different developmental stages exhibit diurnal migrations.

Larvae of six genera, *Penaeus, Parapenaeus, Trachypeneus, Xiphopeneus, Sicyonia,* and *Solenocera,* were encountered and the information on these is presented here. Protozoeal and mysis stages of *Gennadas* and *Artemisia* were collected, and these are new records from the Gulf of Mexico. They were reported by Subrahmanyam and Gunter (1970). The study was conducted from November 1966 to December 1968 inclusive.

MATERIALS AND METHODS

Plankton samples were collected from three depths at six different stations in the Gulf of Mexico. Subject to weather conditions, cruises were made to all or some of the stations every month for the purpose of obtaining a night and a day series of samples.

FIELD PROCEDURE

Stations

The sampling stations were established to provide 18 m depth intervals. Station I was of particular interest because of its location just off the western end of Horn Island, where the depth was 10 m. The exact locations of the different stations are indicated in Fig. 1 and Table 1. The R. V. *Gulf Researcher*, a 65-foot (19.8 m) boat owned by the Gulf Coast Research Laboratory was used for the sampling program.

Equipment

For salinity estimates water samples were collected with Nansen bottles from the two subsurface depths and with a bucket from the surface.

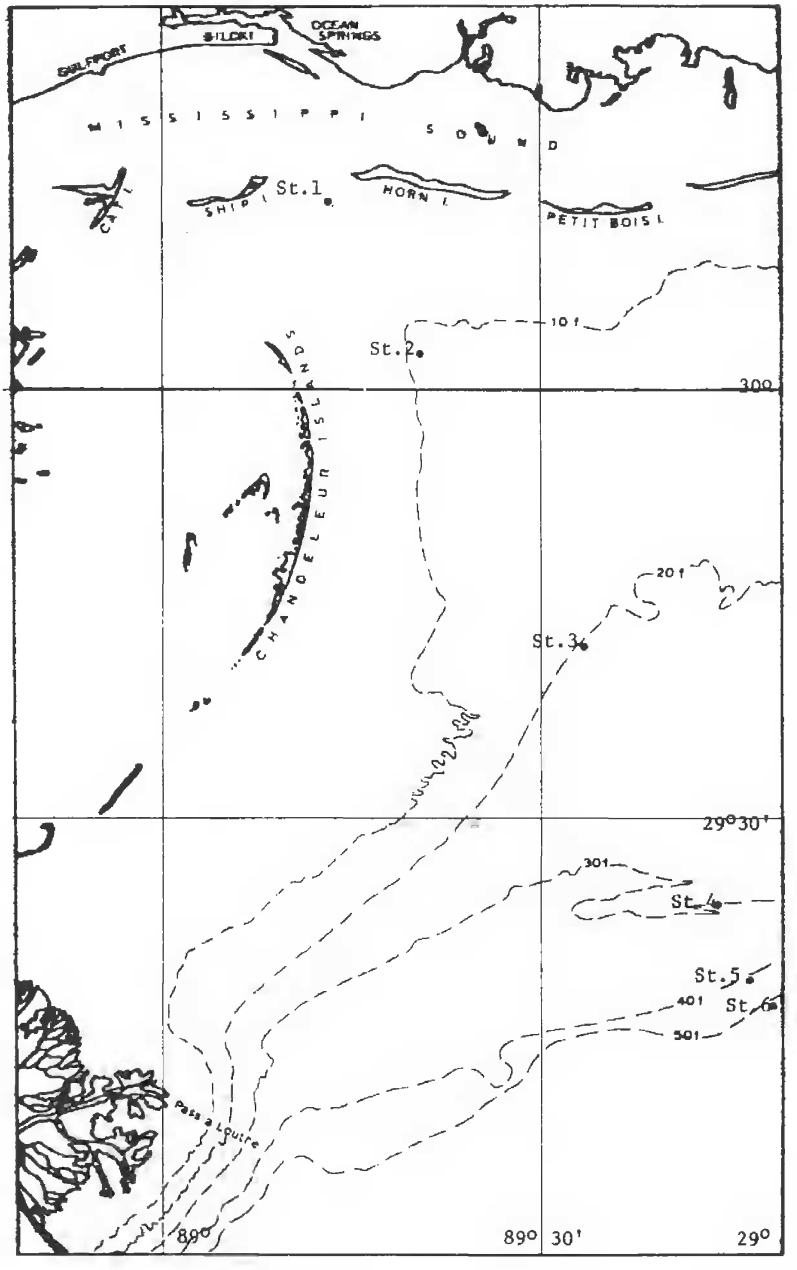

Figure 1. Station locations off the Mississippi Gulf Coast.

Table 1. Station locations and their depths

St. No.	Loran 3HI	3HO	Longitude West	Latitude North	Depth (m)
I	1108	3598	88°47'30"	30°13'15"	10.7
I	1110	3596	88°47'00"	30°12'30"	9.1
II	1220	3580	88°40'15"	30°02'30"	18.3
II	1220	3580	88°40'15"	30°02'30"	20.1
III	1440	3539	88°27'30"	29°42'00"	36.6
IV	1618	3494	88°17'00"	29°24'15"	54.9
V	1657	3480	88°14'00"	29°19'00"	73.1
VI	1683	3472	88°12'05"	29°17'15"	91.5
VI	1556	3457	88°31'00"	29°12'00"	109.8
VI	1562	3449	88°33'00"	29°12'00"	100.6

The positions of the stations were determined by Loran.and the fathometer

NOTE: At times due to the drifting of the boat the Station locations differed slightly. Therefore, the altered positions for St. I, St. II and St. VI are also included in the Table.

Temperature profiles at each station were made with two bathythermographs, one that operated up to about 70 m depth, and the other up to about 275 m. Reversing thermometers mounted on the Nansen bottles offered a check on the bathythermograph temperature readings. Air temperatures were taken with a dry and wet bulb thermometer.

Plankton collections were made with three closing nets devised according to Hardy (1956). Each net measured 50 cm across the mouth, with a cross sectional area of 1964 cm^2, and was 2 m long up to the bucket, including the canvas portion around which the belly rope for closing the net was looped. The netting was No. 3 Nylon with 0.33 mm mesh size. The surface net was towed from the stern of the boat. Simultaneously, the other two nets were towed at two subsurface levels. These two nets were fixed half the station depth apart (e.g., 9 m apart at 18.2 m station) on the same cable, with the bottom net attached 1 m above the sinker. Messengers for closing the nets were fixed on the closing devices. Three minutes were allowed for stabilization of the wire angle. Then the nets were towed at 600 rpm (3 to 5 km/hr) for exactly 20 minutes. At each station a circular course was taken to avoid drifting into deeper or shallower waters. The cable angle was measured at the beginning of each tow and attempts were made to keep the angle constant during the tow. Appropriate lengths of cable, read off a prepared chart, were let out for sampling at the desired depths (cable length=depth x cosecant of wire angle). Later the exact depths were calculated (depth=sine of wire angle x cable length). Since the position of the bottom net was known, and the length of cable sent out corresponded to the depth of the station, the bottom net was usually 1 m above the bottom. The

subsurface nets were always fixed with the same distance between them on the cable, and therefore the sampling depth of the middle net varied a little due to the different cable angles. After the tow was completed a messenger was sent down to close the subsurface nets. At the same time the surface net was hauled aboard. Plankton samples (from the three depths) were stored in separate bottles containing 10% formalin.

In my absence, sampling was done by trained personnel. The number of samples collected and the other details are given in Table 2.

Table 2. Details of the samples collected at 3 depths

Year & Month	Day St.	Number of samples collected: No. samples	Night St.	No. samples	Total
1966					
Nov.	II-VI	15	–	–	15
Dec	I-VI	18	–	–	18
				TOTAL	33
1967					
Jan	I-VI	18	I-VI	18	36
Feb	I-III	9	–	–	9
Mar	I-VI	18	II-III	6	24
Apr	I,II	5	–	–	5
May	I-VI	18	I-VI	18	36
June	I-VI	18	I-VI	18	36
July	I-VI	18	I-VI	18	36
Aug	I-VI	18	I-VI	18	36
Sep	I,II	6	I,II	6	12
Oct	I	3	II,III	6	9
Nov	I,II	6	III-V	9	15
Dec	I	3	I,II	6	9
				TOTAL	263
1968					
Jan	I-III	9	I-III	8	17
Feb	I	3	–	–	3
Mar	I-III,VI	11	IV-VI	8	19
Apr	I,II	6	–	–	6
May	I-IV	10	I-III	9	19
June	I, II, IV-VI	14	III	3	17
July	I-IV	12	I,II,V,VI	11	23
Aug	I-VI	18	–	–	18
Sep	I-III	9	III-VI	11	23
Oct	I-VI	18	I-VI	18	36
Nov	I-VI	18	I-VI	18	36
Dec	I-VI	18	I-VI	15	33
				TOTAL	248
				GRAND TOTAL	544

Trawling was done with a 40-foot (12.19 m) balloon trawl with a mesh size of 3.2 cm from knot to knot. The boat speed was 1100 rpm (14 km/hr) for this purpose. The adult shrimp were picked out and preserved in 20% formalin for later identification.

LABORATORY PROCEDURE

Temperatures at different depths were read off the bathythermograms made at each station. Salinity was estimated with a Goldberg refractometer. The salinity at the depth where the middle net was calculated to be was read off the temperature-salinity curves drawn for each station by the procedure of McLellan (1965).

Plankton samples were allowed to settle for at least 48 hours and the settled volumes were recorded. All the penaeid eggs and larvae were picked out. The larvae were identified as to developmental stages and genera using Cook (1966) and other references. The larvae were stored in vials of 5% buffered formalin.

Since the numbers of larvae caught might be related to the amounts of plankton strained, correlation analysis was made between settled sample volumes and numbers of larvae per 500 ml standard volume. The nonsignificant correlation coefficients, 0.019 and 0.127, respectively, for day and night samples ruled out any such relationship. The numbers of larvae caught apparently depended on their general availability in the water column sampled. Hence the numbers of larvae per sample are compared in terms of catch per unit effort (20 min standard tow).

Adult shrimps were identified, measured, and sexed. Since the maturity condition reveals the breeding potential of the species, the different maturity stages of males and females were determined by methods set forth before (Subrahmanyam 1965b).

RESULTS

HYDROGRAPHY

The two physical factors examined were temperature and salinity. The salinity ranges are given in Tables 3 and 4, and the temperature ranges in Tables 5 and 6.

Salinity

The minimum salinity during the study period was 18.5‰ at St. I and 26.8‰ at St. VI. But the maximum salinities varied between 36.6‰ and 38‰ only. The range of variation decreased seaward, the deeper waters tending to fluctuate over

Table 3. The ranges of salinity (‰) at different stations during 1966-1968.

St.	Depth	Minimum Month	Minimum Sal. ‰	Maximum Month	Maximum Sal. ‰	Range ‰
I	10	Jul. 68	18.5	May 68	36.6	18.1
II	18	Jul. 68	21.8	Nov. 68	37.1	15.3
III	36	Mar. 68	24.4	Oct. 67	37.7	13.3
IV	54	Oct. 68	27.2	Jun. 68	37.2	10.0
V	72	Aug. 68	26.0	Nov. 68	37.7	11.7
VI	90	Oct. 68	26.8	Aug. 67	38.0	11.2

Table 4. The ranges of salinity (‰) at different depths during 1966-1968.

St.	Surface Min.	Surface Max.	Surface Range	Middle Min.	Middle Max.	Middle Range	Bottom Min.	Bottom Max.	Bottom Range
I	13.1	37.1	24.0	19.0	37.6	18.6	19.9	37.6	17.7
II	18.6	37.1	18.5	22.2	38.9	16.7	23.3	38.9	15.6
III	21.6	37.0	15.4	24.6	38.2	13.6	24.6	39.0	14.4
IV	16.8	36.8	20.0	25.0	38.0	13.0	28.8	38.9	10.1
V	18.6	37.4	18.8	25.6	38.0	12.4	24.9	38.0	13.1
VI	23.2	38.0	14.8	23.3	38.0	14.7	26.6	38.0	11.4
Range	10.1	1.2		6.6	1.3		8.9	1.3	

Table 5. Temperature ranges at different stations during 1966-1968.

St.	Depth (m)	Minimum Month	Minimum Temp. °C	Maximum Month	Maximum Temp. °C	Range °C
I	10	Jan. 67	12.3	June 68	30.1	17.8
II	18	Mar. 67	14.2	Aug. 68	29.4	15.2
III	36	Feb. 67	16.2	Aug. 68	30.1	13.9
IV	54	Jan. 68	16.9	June 68	28.5	11.6
V	72	Mar. 68	17.7	Oct. 68	26.4	8.7
VI	90	Mar. 68	17.4	Aug. 68	26.8	9.4

Table 6. Temperature ranges at different depths during 1966-1968.

St.	Surface Min.	Surface Max	Surface Range	Midwater Min.	Midwater Max.	Midwater Range	Bottom Min.	Bottom Max.	Bottom Range
I	12.2	30.4	18.2	12.2	31.0	18.8	12.5	29.5	17.0
II	13.6	30.1	16.5	14.4	28.0	13.6	14.4	29.0	14.6
III	13.6	30.8	17.2	16.1	31.5	15.4	16.4	29.0	12.6
IV	15.6	32.0	16.4	17.2	26.5	6.3	17.2	27.0	9.8
V	17.5	30.4	12.9	17.8	25.9	8.1	17.8	25.5	7.7
VI	17.8	30.4	12.6	17.2	28.0	10.8	17.2	21.9	4.7
Range	5.6	0.3		5.6	5.5		4.7	7.6	

a range of 11.2°/00 as compared 18.1°/00 at St. I. Months of low and high salinities differed among the stations (Table 3).

Surface, midwater, and bottom salinities at each station also showed certain trends. The minimum surface salinity ranged from 13.1°/00 at St. I to 23.2°/00 at St. VI. The midwater salinities fluctuated from 19.0°/00 to 26.6°/00. Minimum salinities were higher toward the bottom, and the range of variation decreased from 10.1°/00 at the surface to 8.9°/00 at the bottom. Maximum salinities at all depths of different stations varied only within 1.3°/00 (Table 4).

No correlation was found between larval abundance and salinity, the correlation coefficients being 0.07 and 0.03, respectively, for day and night collections. In general, salinity fluctuations did not follow predictable patterns.

Temperature

Minimum temperature was recorded in winter in the inshore waters and at St. III and IV, and in spring at St. V and VI. When the average temperature is considered, inshore waters cooled down faster than the offshore waters. For deep waters 16.2 C was the lowest temperature recorded (Table 5). When the minimum temperature is considered, the St. VI minimum was 5.1 C higher than the St. I minimum. Maximum temperatures varied only over a range of 3.7 C. The range of fluctuations during the period of study decreased from 17.8 C at St. I to 9.4C at St. VI. When the stations are compared (Table 6) it is seen that the minimum surface temperature was higher seaward, and the maximum temperature did not vary a great deal. Midwater and bottom minimum temperatures varied up to 4.0 C between St. I and III. At deeper stations variation was only in a range of 0.6 C. However, the range of fluctuations of maximum temperature was greater in midwater and bottom, 0.3 C, 5.6 C and 7.6 C at the surface, midwater and bottom respectively.

Vertical temperature profiles for all the stations are depicted in Fig. 2. Data are from the bathythermographs. In winter, isothermal conditions existed at St. II, IV and VI, and slightly warmer waters occurred toward the bottom of the other stations. In spring, temperature did not vary more than 0.6 C from surface to bottom at St. I, II, and III, while at St. IV and V considerable mixing of cold and warm waters was evident. Ninety meter waters (St. V) showed a gradual decrease in temperature toward bottom. In summer, typical thermoclines were found only at St. I and II. At all the other stations a gradual top to bottom decrease was evident. In fall, vertical mixing and isothermal conditions were evident at St. I through VI with some stratification at St. V and VI.

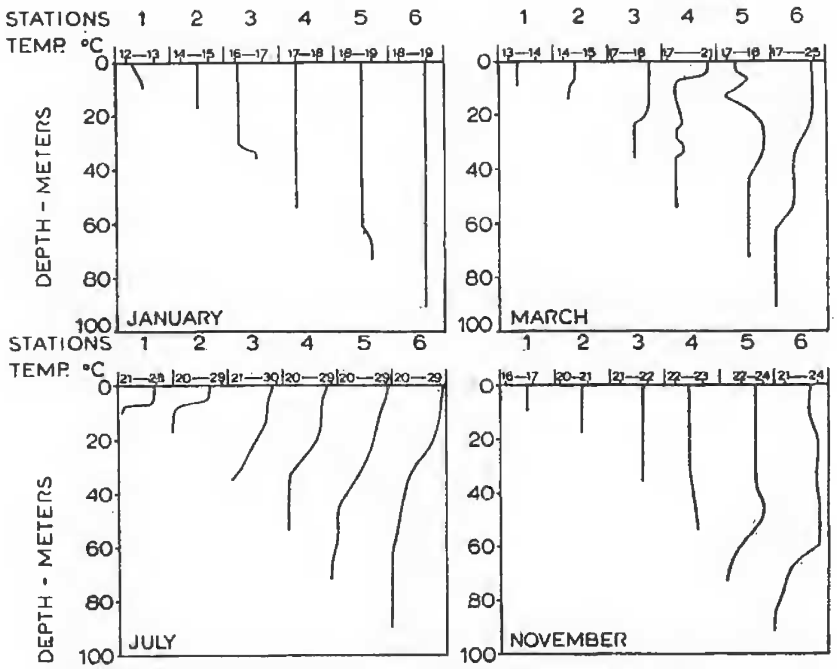

Figure 2. Bathythermograms for six stations in different seasons.

SEASONAL ABUNDANCE AND HORIZONTAL DISTRIBUTION

General

Larvae of the six genera, *Penaeus*, *Parapenaeus*, *Trachypeneus*, *Xiphopeneus*, *Solenocera* and *Sicyonia*, were caught in all depths at all the stations, but the relative abundance of in-

Table 7. Seasonal abundance of penaeid larvae expressed as average number of larvae per 20 min haul

	1967						1968					
Station	I	II	III	IV	V	VI	I	II	III	IV	V	VI
Spring	64	62	30	58	237	42	25	267	30	47	17	43
Summer	47	719	262	115	95	123	68	97	500	72	134	121
Fall	34	117	185	496	161	—	63	707	214	110	85	25
Winter	3	43	78	356	152	230	3	28	19	76	29	36
Average for two years 1967 - 1968.												
Spring	45	165	30	53	127	43						
Summer	57	408	371	94	114	122						
Fall	49	412	200	303	123	25						
Winter	3	36	49	216	91	133						

dividual genera varied in relation to seasons and depth. Average counts for each station and for the four seasons of 1967 through 1968 are given in Table 7.

Large numbers of larvae were taken in winter at stations beyond St. III, peaks being at 36 m depth in early winter and at 54 or 90 m depths in mid-winter.

In early spring the peak was still at St. IV, but by late spring the peak shifted to St. II. Fair numbers of larvae were caught at all stations during summer, indicating that penaeids were breeding over a wide area.

In fall, the peak was still at St. II but increased numbers were taken from deeper stations, for example at St. IV.

In winter, larvae were scarce at St. I to III and good numbers were taken at St. IV, V, and VI.

These trends in shifting of the larval peaks become clear if the average counts for the two years are examined (Table 7). Shrimp appeared to spawn in shallow or deep waters with warming or cooling of the environment. In spring spawning activity seemed to be concentrated at 18 m, in summer at 18 and 36 m, in fall at 54 m and in winter beyond 36 m. Minor spawning activity was evident at the other depths.

Correlation studies relating larval abundance and absolute *in situ* temperatures at various depths and stations failed to show any significant correlation, the correlation coefficients being 0.09 for day and 0.08 for night samples. This is to be expected in view of the fact that spawning activity heightens or even starts in spring in the inshore waters, when temperature starts rising, while in deeper waters it occurs all through the year. Table 8 indicates that shrimp in this area breed between average temperature range of 17 and 29 C. Within this range the spawning activity of the six genera, as indicated by the lar-

Table 8. Average seasonal temperatures (°C) at different stations during 1967-1968.

	1967						1968					
Station	I	II	III	IV	V	VI	I	II	III	IV	V	VI
Spring	21.4	19.5	20.1	20.7	20.4	20.6	22.2	20.8	19.6	20.1	18.0	19.3
Summer	25.3	23.3	24.1	23.9	22.4	22.6	29.5	28.2	28.4	25.7	24.9	24.6
Fall	23.2	23.3	22.6	21.3	21.6	—	21.0	23.8	24.5	22.9	23.2	22.7
Winter	14.6	15.8	16.9	18.3	19.3	19.1	13.9	16.0	17.1	19.6	21.9	21.6
For Two Years 1967 - 1968.												
Spring	21.8	20.2	19.9	20.4	19.2	19.9						
Summer	27.4	25.8	26.2	24.8	23.6	23.6						
Fall	22.1	23.6	23.6	22.1	22.4	22.7						
Winter	14.2	15.9	17.0	19.0	20.6	20.4						

val abundance, varies in such a manner that specific correlation with *in situ* temperatures may not show. In other words, larval abundance is not absolutely related to temperature changes between 17 and 29 C.

Table 9. Bottom temperatures (°C) at different stations in four seasons during 1967 - 1968.

	1967						1968					
Station	I	II	III	IV	V	VI	I	II	III	IV	V	VI
Spring	20.7	18.3	19.3	19.5	19.5	17.6	21.7	19.3	19.2	19.4	17.8	18.3
Summer	24.0	21.5	21.0	21.3	19.6	19.4	29.1	26.8	27.1	22.7	21.5	19.2
Fall	22.4	23.2	22.8	21.7	19.5	—	20.5	24.4	24.1	21.5	21.3	21.0
Winter	14.6	16.1	18.1	18.6	19.4	18.6	14.7	16.4	17.8	20.4	22.0	21.5
For Two Years 1967 - 1968.												
Spring	21.2	18.8	19.2	19.4	18.6	18.0						
Summer	26.6	24.2	24.1	22.0	20.6	19.3						
Fall	21.4	23.8	23.4	21.6	20.4	21.0						
Winter	14.6	16.2	18.0	19.5	20.7	20.1						

As penaeid shrimp are benthonic, bottom temperature is important for their spawning. It is evident from Table 9 that intense spawning occurred within the temperature range of 17 to 29 C. In spring, summer and fall, all six genera appear to breed in waters up to 54 m (temp 18.8 to 24.2 C) and in winter to shift their spawning area to deeper waters where the temperature remained above 19 C. From the present data, penaeids seem to spawn throughout the year, but they move to deeper waters as the season advances from spring to winter. This does not, however, mean that one species spawns all the time. Presence of larvae in plankton is a good indication of spawning activity even in temperate waters as has been shown for the European oyster (Korringa 1957).

Abundance in relation depth

Station I (10 m). The trends in abundance and seasonal distribution of the larvae are depicted in Fig. 3.

Larvae, mostly of four genera, started appearing in fair numbers in May and were present until November. The maximum number taken in one haul was 192 (September 1968, day). Four per cent and 6.3% of all the larvae caught occurred at this station in 1967 and 1968, respectively. This was a unimodal trend of abundance, larvae being caught between May and November in good numbers. Bottom temperature rose from 13.3-15.5C to 21.7-23.1C in April, and dropped in the October-November period from 20.8-23.2 to less than 17 C. These periods of rising and falling temperatures produced more numbers of

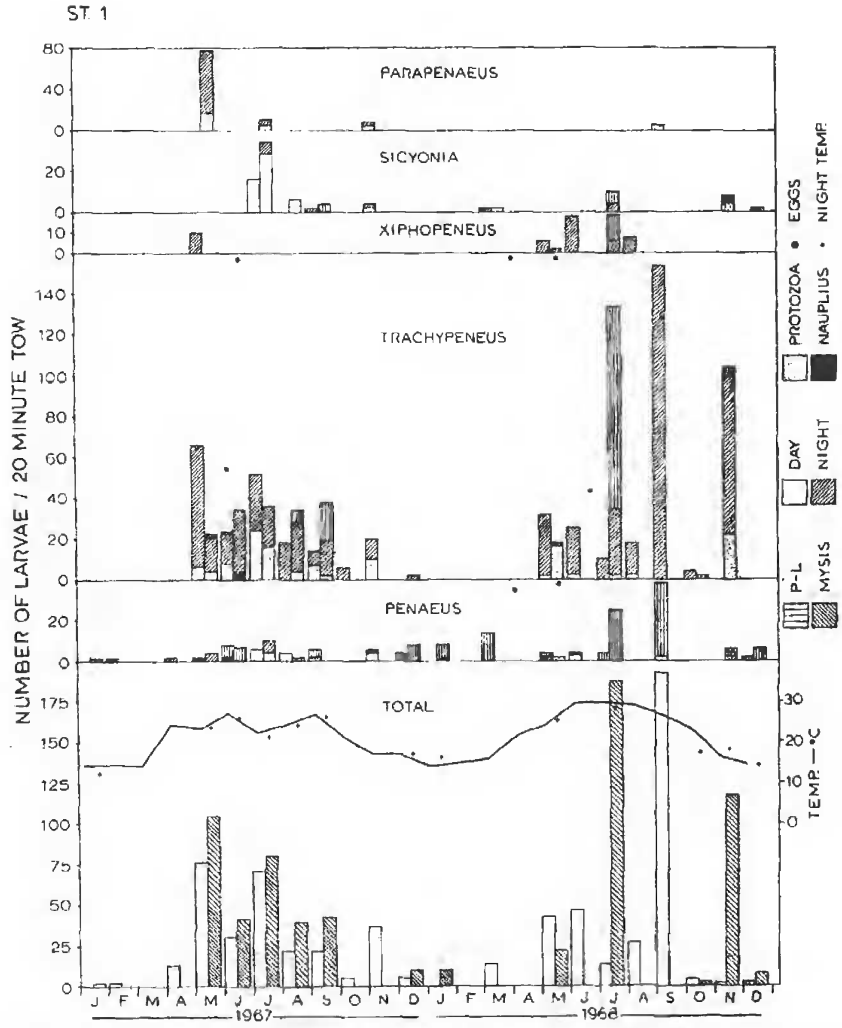

Figure 3. Seasonal abundance, stage and generic composition of penaeid larvae at Station 1 during 1966 to 1968.

larvae. Peaks of abundance were in May to September and in November, i.e., spring-summer and fall peaks. In general, more larvae were caught at night.

Trachypeneus was the dominant genus, the number of larvae ranging from 2 to 153 per haul. The spawning season started by April and lasted through November. Spring-summer and fall peaks were evident. Eggs were taken in April (275) and May (40,340) of 1968, and in June (283) 1967; nauplii in June;

protozoeae in all months except October; myses in all months; and postlarvae in July, August, September and November.

Second in the order of abundance was *Penaeus*, the number of larvae varying from 1 to 38 per haul. The breeding season started in April and continued until November. Eggs, probably of white shrimp, were taken in April (35) and May (450) of 1968. Before May only postlarvae of brown shrimp were obtained. White shrimp postlarvae were caught from May to November, but in December only brown shrimp postlarvae occurred. Protozoeal and mysis stages first appeared in May. Nauplii occurred only in June. On the basis of the stages of larvae, spawning occurred from April to November.

Sicyonia ranked third in numbers, the maximum number of larvae caught being 34 per haul. Though all the four stages were taken in good numbers, protozoeae were dominant in July and August 1968. The spawning activity appeared to last from March through November.

Xiphopeneus occurred mostly as myses and only in five months. The maximum number caught was 20 per haul. Spawning occurred from May to August.

Parapenaeus is known to be a deep water genus (Cf. Williams 1965). Fair numbers of larvae were taken in May 1967 (78 per haul). Protozoeal and mysis stages were observed at this time, and in July and November also a few of these two stages were caught.

To summarize the trends, spawning of all the species of shrimp appears to begin in April, with rising bottom temperatures and continue through summer and fall. Decreasing temperature in November seems to induce spawning again. This is chiefly a unimodal trend, because spawning continues, once it starts, without a break within the season. *Trachypeneus spp.* were dominant and *Penaeus spp*, next in abundance. *Sicyonia* is fairly common at these depths, and the occurence of *Parapenaeus* is considered unusual.

Station 11 (18 m). The greatest numbers of larvae were obtained at this station. The peaks were much pronounced (Fig. 4). The proportion of larvae as percentage of all larvae captured, amounted to 37.8 for 1967 and 42.3 for 1968. Larvae of five genera started appearing in appreciable numbers (over 100 per haul) in May and continued through November. The maximum number obtained was 2543 per haul in October 1968. Peaks were in June and July 1967, and in May, July and October 1968. Indications of spawning activity were apparent in January, but pronounced spawning occurred from May through November. This again is a unimodal trend of spawning. The temperature range during this period was between 19.4 (Novem-

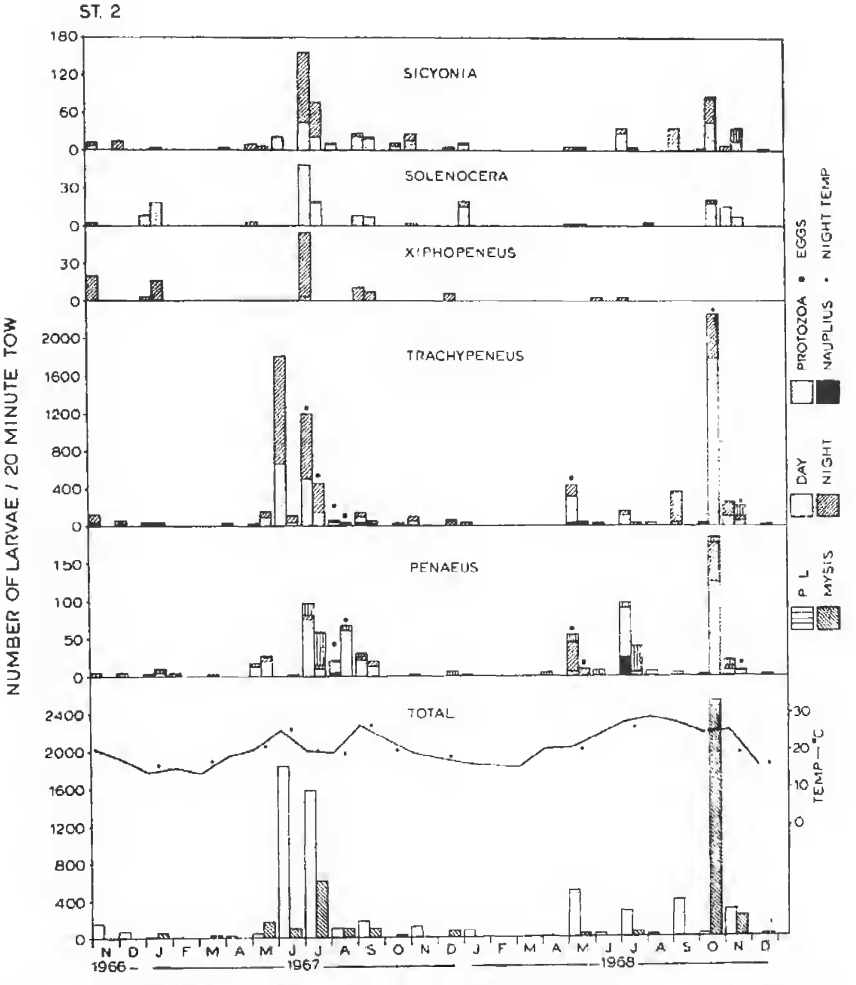

Figure 4. Seasonal abundance, stage and generic composition of penaeid larvae at Station 2 during 1966 to 1968.

ber 1968) and 27.7 C (July 1968). A few early larvae were taken in January when the temperatures were 16.1 and 16.9 C in 1967 and 1968 respectively.

As at the previous station, *Trachypeneus* predominated, maximum number of larvae taken being 2252 per haul (October 1968). Eggs were obtained in July (240) and August (278) of 1967, and in May (1652), October (90), and November (20) of 1968. Nauplii were taken in September 1967 and May 1968. Protozoeae occurred in all months; myses predominated in summer

and postlarvae appeared in November (Fig. 4). Spawning appeared to have occurred from May through November, and the fall peak was higher than the summer peak.

Penaeus ranked next in abundance, maximum number of larvae taken being 184 per haul, a higher number than caught at St. I. Eggs were taken in August (52) of 1967 and in May (51) and November (10) of 1968. Nauplii occurred in July 1968 and in August 1967. Protozoeae appeared from January to November, and all three stages were caught in varying proportions during the summer and fall months. *Penaeus* species appeared to breed from January to November, with peak activity in summer and fall, the fall peak being higher. Postlarvae of brown shrimp were common in winter, of brown, pink and white shrimp in summer, and again brown and white shrimp in fall.

The next in importance was the genus *Sicyonia*, with a maximum larval production of 155 per haul. Protozoeae started appearing in plankton by March and myses were found throughout. Postlarvae appeared in November. Species of this genus appeared to breed throughout the year with pronounced activity in summer and fall (July and October) at 18 m station.

Xiphopeneus appeared in 7 months and only in the mysis stage. Summer (July) and late fall (November) were peak breeding months. Maximum number of larvae taken was 53 per haul.

Solenocera was the new element taken at this depth. A maximum of 48 larvae per haul was taken. Protozoeae occurred in all the months, especially July, September, October and November. Spawning season appeared to last from January to November with peaks in summer and late fall.

Parapenaeus occurred only twice, in December 1966 and July 1967. All the larvae were protozoeae.

From the foregoing it is seen that breeding starts earlier than May, even in January at 18 m. *Penaeus* occurs in greater abundance, and *Solenocera* starts appearing regularly. Minimum temperature at which spawning occurs is 16.1 C, especially for *Solenocera*.

Station III (36 m). Fairly large numbers of larvae were taken in these waters, the largest number being 1456 per haul (August 1968). Of the total larvae taken during the 2 years 21.2% and 27.1% were collected at this station in 1967 and 1968 respectively. The bottom temperature range was 16.4 C (March 1968) to 29 C (August 1968). Spawning activity of one species or the other was evident throughout the year, with peaks in July, August, November and December. Intense activity started much later than it did at St. I and II. Heightened spawning in December and January was the interesting feature. The trends in larval abundance are illustrated in Fig. 5.

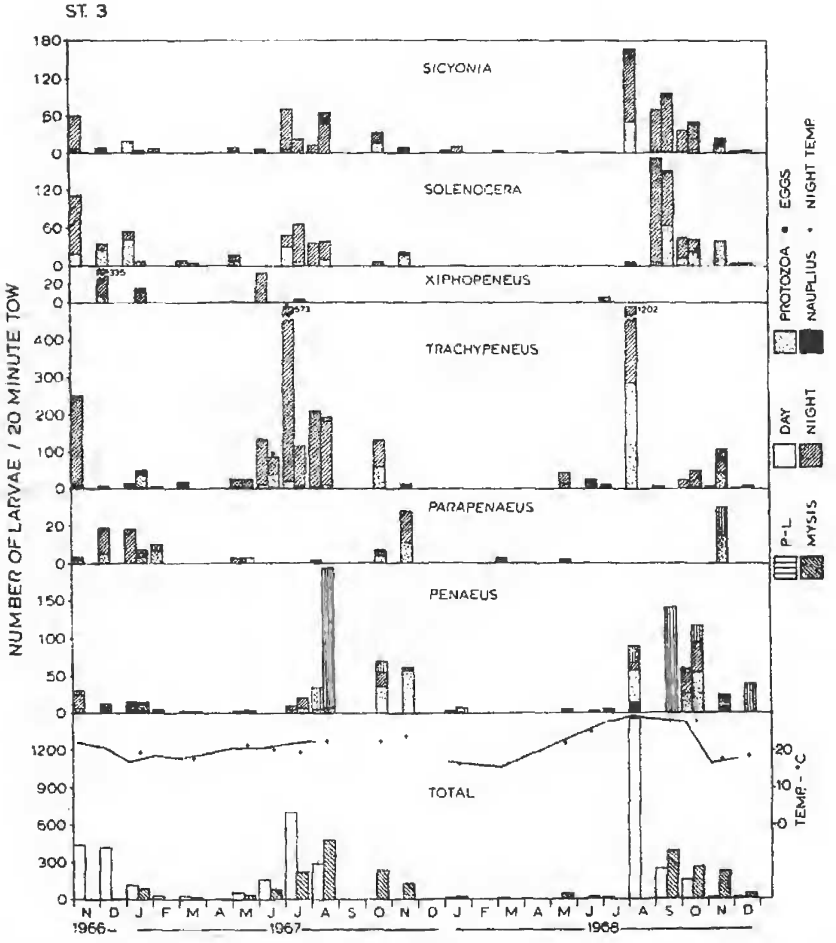

Figure 5. Seasonal abundance, stage and generic composition of penaeid larvae at Station 3 during 1966 to 1968.

Trachypeneus was still the dominant genus, with a maximum density of 1202 larvae per haul (August 1968). Eggs were obtained in June (72) and July (10) of 1967 and May (105) 1968. Protozoeae, as well as myses, occurred in every month, myses being particularly abundant in summer and fall. It appeared that the species of this genus had summer and fall peaks in spawning activity, a bimodal trend, with a less intense period in between the two seasons.

Next in abundance was *Solenocera*, with an observed maximum density of 172 larvae per haul (September 1968). Pro-

tozoeae and myses were taken in almost all months. Pronounced spawning occurred in January and in March through December, which amounted to year round spawning with distinct periodicity.

Sicyonia ranked third in abundance, with a maximum of 166 larvae per haul (August 1968). Protozoeae and myses occurred throughout the period of study, and postlarvae were abundant in August and November. Peak spawning occurred during July through November. Spawning on a smaller scale in winter was also evident.

Penaeus contributed to a fair proportion of larvae, with a maximum of 141 larvae per haul. Spawning started in May and continued through December. In January minor spawning activity was apparent. Protozoeae and myses occurred during summer, fall and winter. A bimodal pattern of breeding intensity was obvious, with peaks in July-August and October-December. Brown shrimp postlarvae were taken from January to March 1967, and in January and June through December 1968. White shrimp postlarvae were abundant in August 1967 and September 1968.

Parapenaeus was a stable element at this depth. Protozoeal and mysis stages were caught in almost all the months. Maximum number of larvae obtained was 30 per haul in November 1968. Two periods of intense spawning were observed, January-February and October-December, which was indicative of fall and winter spawning.

Xiphopeneus occurred sporadically, with a peak in December 1966, when 338 larvae per haul were taken.

To summarize, breeding activity of different species is evident throughout the year. This is due to the occurrence of summer-fall spawners, and fall-winter spawners in these waters. *Parapenaeus,* which is a permanent element at this depth, appears to be mainly a fall and winter spawner.

Station IV (54 m). The maximum number of larvae taken at this depth was 496 per haul. The total numbers caught amounted to 13.5 and 9.9 per cent of all the larvae taken in 1967 and 1968, respectively. Year round spawning activity was evident with peaks in summer, fall and winter. Bottom temperatures ranged from 17.2 C in January 1967 to 23.0 C in October 1968. The fluctuations in abundance of larvae of the six genera are depicted in Fig. 6.

The deep water genus, *Solenocera,* was the dominant element, with a maximum of 212 larvae per haul (January 1967). Protozoeae and myses occurred in all the months, and myses were particularly abundant during summer. Starting off with

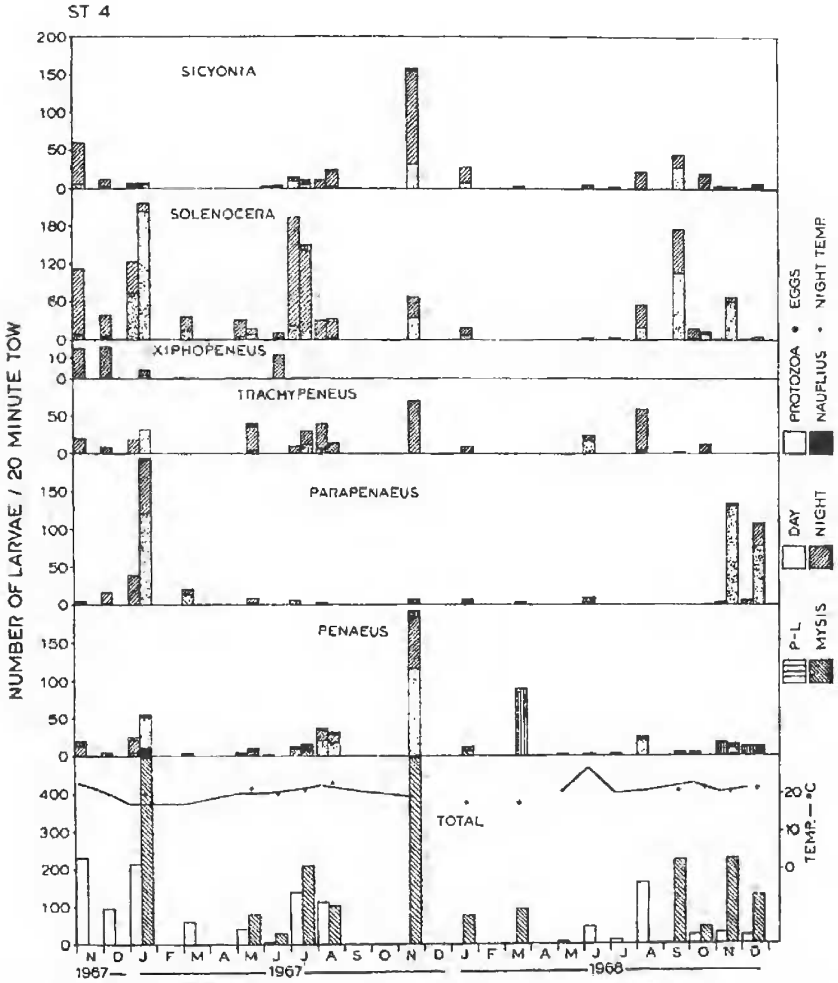

Figure 6. Seasonal abundance, stage and generic composition of penaeid larvae at Station 4 during 1966 to 1968.

a January peak, spawning heightened in summer, continued through September, and again reached a peak in November. Year round activity was evident.

Parapenaeus was next in importance, the maximum number caught being 193 larvae per haul (January 1967). Protozoeae occurred mainly in January, March, June, November and December. Again there was an indication that species of this genus mainly bred in fall and winter, with minor activity in spring and summer.

Penaeus larvae occurred in good numbers, the maximum being 191 per haul (November 1967). Nauplii were taken in January 1967. Spawning started in January, as evidenced by the occurrence of protozoeae and myses, and peak activity was found in August, November and January. Summer, fall and winter spawning was evident. Postlarvae of white shrimp were plentiful in July 1967 and March 1968. Brown shrimp postlarvae appeared in fair numbers in March 1968.

Sicyonia larvae were reasonably abundant, the maximum being 159 per haul. Protozoeae occurred chiefly from July through December except in October and November. Summer, fall and winter spawning was apparent, with peaks in August, September and November. In these waters, the species of the genus appeared to be mainly fall and winter spawners.

Trachypeneus showed a marked decline in numbers of larvae, the maximum caught being only 70 per haul (November 1967). Protozoeae were less abundant than myses. Spring, summer and winter spawning was evident.

Xiphopeneus were least abundant, maximum being 16 larvae per haul. Protozoeae were scarce and myses occurred only in 4 months.

It is seen from the foregoing that deep water species, *Solenocera* and *Parapenaeus* spawn intensely at this depth. Year round breeding and a bimodal trend of larval abundance are apparent.

Station V (72 m). The maximum caught at this depth was 542 larvae per haul (March 1967). Breeding activity was evident in all the months sampled as can be seen from Fig. 7. Of the total larvae captured 9.4 and 8.4% were obtained in samples from this station. The temperature range on the bottom was 17.8 C in March 1968 to 25.5 C in October 1968. Intense breeding occurred in January, March, July, August, October and November.

Solenocera was the dominant genus, with a maximum density of 356 larvae per haul (March 1967). Protozoeae were taken in all the months except June, and myses occurred throughout the year. Spawning was pronounced during winter, spring and fall.

Parapenaeus was next in the order of abundance, the maximum number of larvae caught being 177 per haul (March 1967). Protozoeae were observed mainly in January, March, May, August, November and December. Myses occurred in all seasons. Peak numbers were taken in January, March and August, which indicated winter, spring and fall spawning for the species of this genus.

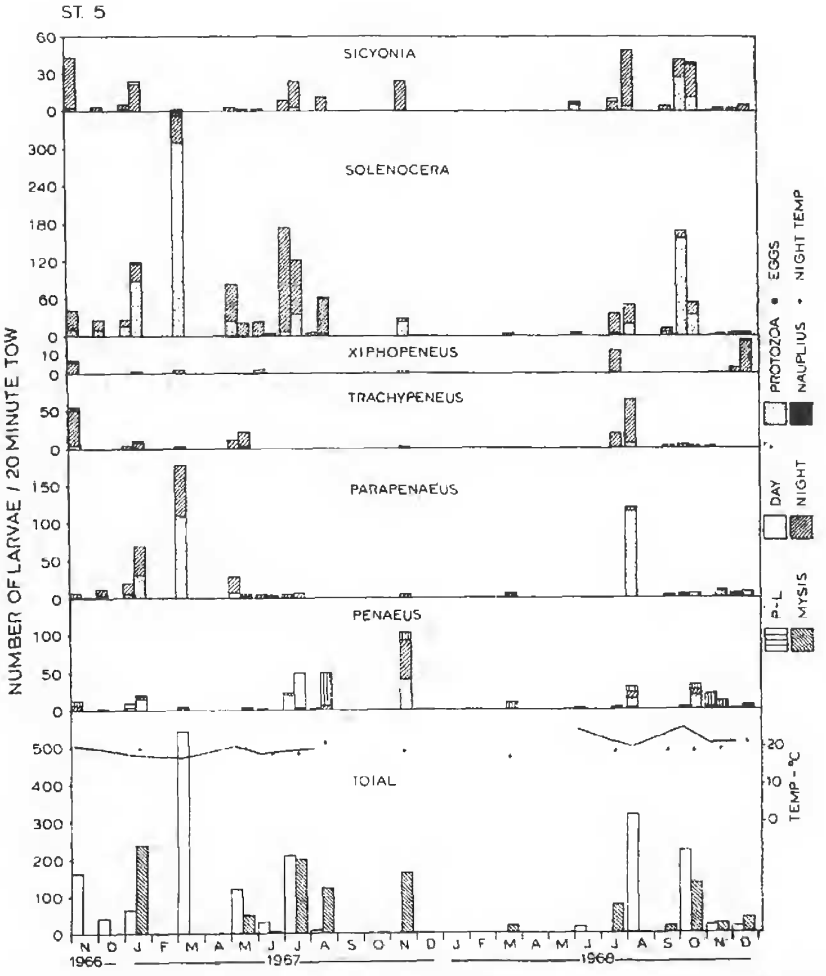

Figure 7. Seasonal abundance, stage and generic composition of penaeid larvae at Station 5 during 1966 to 1968.

Penaeus larvae were taken in fair numbers, maximum being 103 per haul (November 1967). Protozoeae appeared all through except in March and June when postlarvae were dominant. The same was true for myses. Postlarvae of brown shrimp occurred in October and November 1968, and of white shrimp in August mainly. Spawning was marked in January, July and August through November.

Sicyonia larvae were taken in small numbers, maximum being 52 larvae per haul. Protozoeae appeared in May, July-August, and October-November, and myses were present in all

seasons. Year round spawning with peak activity in January, July, August and October-November was apparent.

Xiphopeneus was represented only by myses in 7 months. The maximum number caught was 18 per haul. The species appeared to breed from August to December at this depth.

Trachypeneus larvae were taken sporadically, the maximum being 63 per haul (August 1968). Protozoeae were rare compared with myses.

From the foregoing, the spawning season for all the species appears to be protracted, and breeding occurs even in winter. *Solenocera* species still dominate at this depth.

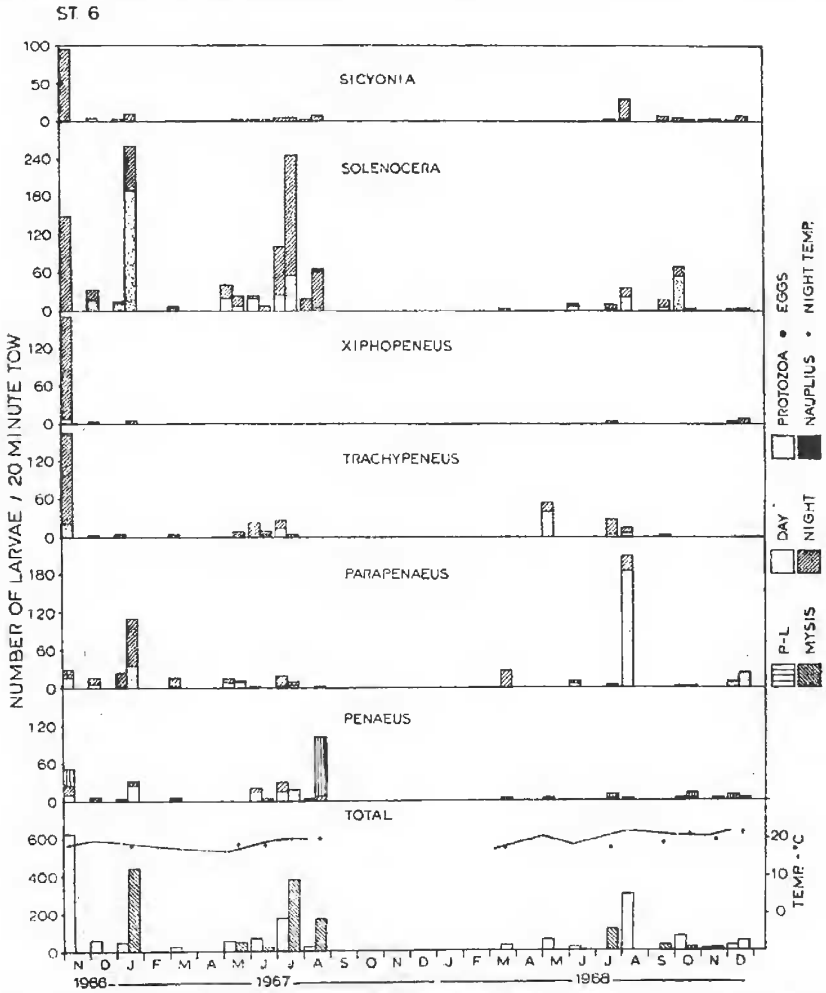

Figure 8. Seasonal abundance, stage and generic composition of penaeid larvae at Station 6 during 1966 to 1968.

Station VI (90 m). Data from this station are not complete, but the available information indicated year round breeding activity (Fig. 8). Larval abundance was pronounced in January, July 1967, August 1968 and November 1966. Bottom temperature varied between 17.2 (March 1968) and 21.9 C (August 1967). The maximum number of larvae taken was 642 per haul (November 1966).

Solenocera was dominant at this station also, with a maximum density of 260 larvae per haul (January 1967). Protozoeae and myses occurred in all the months. Peak abundance was noticed in January, July, and October-November.

Next in importance was *Parapenaeus*, the maximum number of larvae taken being 208 per haul (August 1968). Protozoeae and myses were taken in all months. Protracted spawning activity, with peaks in January, July-August, and November-December, was evident.

Trachypeneus larvae occurred in fair numbers, with a maximum density of 166 larvae per haul. Protozoeae were taken in all months except January and October, and myses occurred throughout. Peak spawning activity was noticed in June-July and November.

Xiphopeneus was observed sporadically, and the maximum number of larvae collected was 159 per haul. Peak numbers occurred in November 1966.

Penaeus larvae occurred in moderate numbers, the maximum taken being 101 per haul (August 1967), and the majority were postlarvae. Protozoeae appeared in all months except August, and myses appeared throughout the year. Postlarval brown shrimp were taken during November and December and white shrimp in August.

Sicyonia was the least abundant genus, with a maximum density of 91 larvae per haul (November 1966). Very few protozoeae were taken and myses occurred in all months. The peak spawning seasons appeared to be August and November.

At this station *Solenocera* was still the dominant genus. Protracted spawning activity with winter breeding is observed at this depth.

When the trends in larval abundance at all depths are considered certain patterns become apparent. While spawning activity starts only in spring at 10-m depth, it starts earlier, even in January, at greater depths. Further, a unimodal pattern of abundance is characteristic of 10-and 18-m depths, and a bimodal trend is seen in deeper waters. A gradual replacement of species is obvious as station depth changes. *Trachypeneus* larvae occur abundantly at 10, 18 and 36 m, and *Solenocera* larvae at 54, 72 and 90 m. *Penaeus* appear in fair numbers at 18 m.

and on either side of this depth larval numbers decrease. *Sicyonia* larvae occur in fair numbers at 10 to 36 m, and the density per haul decreases with increasing depth beyond 36 m. *Parapenaeus* larvae occur rarely in waters shallower than 36 m, but in 54, 72 and 90 m waters larval abundance is second only to *Solenocera*. These trends in the horizontal distribution of the larvae show good relationship with the bathymetric distribution of adults of the species of the six genera.

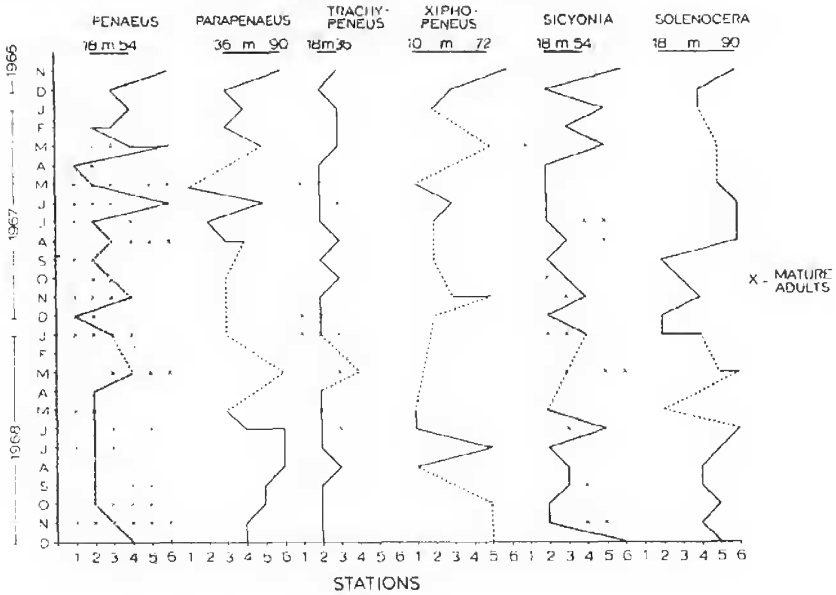

Figure 9. Spawning loci of the six genera in different seasons, within their bathymetric range, as indicated by the larval maxima. (Dotted line indicates no data)

Spawning loci of the species

It is to be expected that different species spawn within the range of their bathymetric distribution. Maximal numbers at any specific depth may indicate the center of spawning activity even though larvae can occur at other depths. In Fig. 9 maximal numbers for each genus are plotted in relation to stations, along with the areas where mature adults were captured. This depiction brings out certain trends in the shifting of spawning centers with respect to seasons.

Penaeus. In warmer months (April to November) larval maxima occurred at 10 to 54 m, and mostly at 18 m. In early spring and winter months peak numbers were caught at 54 to 90 m. The shifting of breeding center closer to shore in warm months was apparent.

Secondly, adults of white, brown and pink shrimp were taken at all or some of the stations, but larval maxima were observed only at specific depth in a specific month.

The bathymetric distribution of the three species of *Penaeus* is known to be: white from inner littoral to 78 m, brown from inner littoral to 128 m and pink to 109 m (Burkenroad 1939, Eldred *et al.* 1961, Williams 1965, and Saloman, Allen and Costello 1968).

The frequency of capture of the three species during the present investigation is given in Table 10.

Table 10. Catch frequency of adults of **Penaeus** species

Station	I	II	III	IV	V	VI
White	8	8	8	1	1	0
Brown	9	13	15	9	9	7
Pink	7	7	1	0	0	0

It is seen from Table 10 that white shrimp concentration was in 10 to 36 m, brown in 10 to 90 m and pink in 10 to 18 m. Probably the summer and fall peaks at 18 m were due to any or all of the three species; those at 36 m due to white or brown shrimp; and those at 72 m and 90 m in winter due to brown shrimp alone. It is also possible that these species may move into deeper waters in colder months to breed there. It is known that white shrimp migrate into deeper waters in winter and a few larvae of pink shrimp have been taken in 180 to 300 m depths off Florida (Eldred *et al.* 1965). Also, each species may have 'preference' for a particular depth as it has been shown in British species of *Leander* (Gurney 1924).

Parapenaeus. Parapenaeus longirostris is the most abundant species of the genus in the Gulf of Mexico, occurring in depths of 25 to 145 m (Burkenroad 1939, Williams 1965), and *P. americanus* occurs in waters deeper than 200 m (Springer and Bullis 1956). Adults of neither species were caught during the present study. Larval maxima were noticed between 36 m and 90 m stations (Fig. 9). A positive correlation between larval abundance and station depth was found for this species.

Trachypeneus. Trachypeneus similis was the only species encountered in trawl catches, but *T. constrictus* also occurs in the study area (Burkenroad 1939). The bathymetric range of these

two species is 20 to 37 m for *T. similis* and 5 to 55 m for *T. constrictus* (Burkenroad 1939). *T. similis* were taken at 10 to 36 m.

Larval maxima occurred in 18 to 36 m depths. In summer larval concentrations were noticed mostly at 18 m and during other seasons at 36 m.

Xiphopeneus. Xiphopeneus kroyeri is the only species of the genus and it occurs mainly in 5 to 36 m (Williams 1965). Larval maxima were observed at 10 to 72 m. Generally, peaks were observed at 10 to 18 m in summer and at 72 m in fall.

Sicyonia. Sicyonia dorsalis, S. stimpsoni and *S. brevirostris* are the three species of the genus in these waters. In trawls both the first and the third species were taken, but *S. dorsalis* was more common. Both the species are known to occur in waters 5 to 85 m deep (Williams, 1965). Larval maxima were mainly restricted to 18 to 54 m, and occasional pulses were noticed at 72 and 90 m (Fig. 9). During summer and fall the concentration of larvae was at 18 to 36 m and in November 1966, and December 1968 it was at 90 m.

Solenocera. Solenocera vioscai, S. atlantidis and *S. necopina* are known to occur off Mississippi, with a bathymetric distribution of 36-72 m, 18-329 m and 5-183 m, respectively (Williams 1965). Generally larval pulses were noticed in depths beyond 54 m during warmer months, and at 18-36 m during cooler months. A positive correlation between abundance and station depth was found for this genus. Species of *Solenocera* are reported to be generally oceanic (Burkenroad 1936).

Larval abundance in relation to occurrence of adults

Most of the statements on the breeding seasons and spawning localities for shrimps are based on the occurrence of mature adults. Therefore, the relationship between the larval distribution and adult concentrations was examined. Table 11 shows that several times, at different stations, mature adults were taken where larvae were absent. Also, larval maxima and adults did not occur in the same area several times (Fig. 9). Only nauplius and protozoea stages were considered for this correlation study, because their motility is negligible. No significant correlation coefficients for the numbers of larvae and mature adults were found. This indicates that mature adults and larvae need not necessarily occur in the same area, and the locations of adult concentrations do not necessarily indicate precise spawning areas.

Table 11. Numbers of mature adult species and larvae(nauplius and protozoea) caught during 1967-1968.

Date	Genus St.	D/N	Penaeus Larvae	Penaeus Adults	Trachypeneus Larvae	Trachypeneus Adults	Sicyonia Larvae	Sicyonia Adults
1967								
Mar. 2	I	D	—	—	—	—	0	1
Mar. 2	II	D	0	1	—	—	—	—
Mar. 21	III	D	0	1	—	—	—	—
Mar. 21	III	N	0	42	—	—	—	—
Mar. 15	VI	D	4	3	—	—	—	—
Apr. 18	II	D	0	1	—	—	—	—
May 18	I	N	0	13	18	2	—	—
May 19	II	D	19	46	1	3	—	—
May 21	VI	N	0	21	—	—	—	—
May 25	III	N	0	9	—	—	—	—
May 25	V	N	1	23	—	—	—	—
June 5	I	N	0	46	—	—	—	—
June 5	II	N	0	12	—	—	—	—
June 22	III	N	0	14	40	14	—	—
June 27	VI	N	3	29	—	—	—	—
July 6	I	N	0	77	—	—	—	—
July 6	II	N	8	45	—	—	—	—
July 25	IV	N	8	10	—	—	6	72
July 12	V	N	—	—	—	—	13	26
Aug. 9	V	D	—	69	—	—	—	—
Aug. 30	IV	N	19	101	—	—	—	—
Aug. 29	III	D	4	5	—	—	—	—
Aug. 8	V	N	—	—	—	—	0	44
Aug. 9	VI	D	0	12	—	—	—	—
Sept. 7	I	N	0	67	—	—	—	—
Sept. 7	II	N	14	92	—	—	—	—
Oct. 27	II	N	6	33	—	—	0	4
Oct. 27	III	N	34	115	—	—	—	—
Nov. 9	I	D	4	51	—	—	—	—
Nov. 14	II	D	2	7	—	—	—	—
Nov. 14	II	N	59	103	—	—	5	1
Nov. 14	IV	N	115	3	—	—	32	7
Dec. 13	I	D	0	53	0	13	—	—
Dec. 5	I	N	0	24	—	—	—	—
Dec. 5	II	N	0	33	2	110	0	3
1968								
Jan. 15	I	N	1	22	0	13	—	—
Jan. 15	II	D	0	31	0	16	0	10
Jan. 17	III	D	0	45	0	2	—	—
Jan. 17	III	N	0	86	—	—	0	5
Jan. 18	IV	N	7	1	—	—	—	—
Mar. 26	III	D	0	9	0	3	0	1
Mar. 26	IV	N	0	1	—	—	0	5
Mar. 27	V	N	0	2	—	—	0	15
Mar. 27	VI	N	0	36	—	—	—	—
May 28	II	N	10	62	10	18	3	5
May 29	I	N	1	22	—	—	—	—
June 19	V	D	0	5	—	—	—	—
June 18	III	N	0	26	10	1	0	2
July 31	I	N	0	85	—	—	—	—

POSTLARVAL ABUNDANCE IN RELATION TO LARVAL OCCURRENCE

Although larval stages of the three species of *Penaeus* cannot be distinguished from one another, an idea of spawning activity of a particular species might be obtained if postlarval abundance is studied. For this discussion only the postlarvae of white and brown shrimp are considered because of their general availability. Average numbers of larvae and postlarvae per haul (for all stations combined) are plotted in Fig. 10.

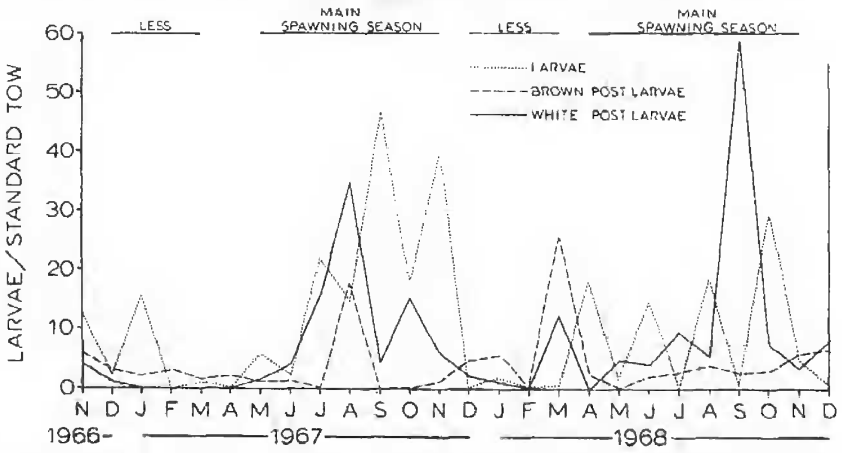

Figure 10. Seasonal abundance of the postlarvae of *Penaeus fluviatilis* and *P. aztecus* in relation to the larval abundance in 10 to 90 m during 1966 to 1968.

The figure shows that the main spawning season for *Penaeus* lasted from April or May to November, with less intense spawning during January to March. During the main spawning season every spawning success was followed by a dip during next month (Fig. 10). Each postlarval peak, either of brown or white shrimp, coincided with dips in larval occurrence. In other words, postlarvae were abundant following each larval peak, which is to be expected because it takes about 10 to 12 days for the nauplii to become postlarvae in summer (Johnson and Fielding 1956). Larval and postlarval peaks were observed in the pattern shown in Table 12.

From the data presented it appears that brown shrimp spawned more intensely in January, March and October, and white shrimp in April, June and August. This does not, however, imply that the two species spawned in succession. Larval peaks of white were observed in shallow waters, and those of brown shrimp in deeper waters. Further, mature adults of *P. fluviatilis* were more frequently caught at 10 and 18 m, while

Table 12. Comparison of larval and white and brown postlarval peaks

Larval peaks		Postlarval peaks	
		White	*Brown*
1967	January		February
	March		April
	May	June	
	July	August	August
	September	October	
	November		December
			January
1968	January	March	March
	April	May	
	June	July	
	August	September	
	October		November
			December

those of *P. aztecus* were taken at 10 to 90 m during warm months and at 36 to 90 m during winter months. *P. duorarum* was found mostly at 10 to 18 m. Temple and Fischer (1967) arrived at the same conclusion concerning the spawning areas of the three species.

VERTICAL DISTRIBUTION

Penaeid eggs are demersal (Pearson 1939, Dobkin 1961, and Subrahmanyam 1965a). Thus, if there is no spring or vernal mixing of waters the early stages may be expected to be found closer to the bottom, and older stages towards surface. The only available information on the vertical distribution of penaeid larvae has been given by Temple and Fischer (1965).

The data on the depth distribution of protozoeal, mysis and postlarval stages are illustrated in Fig. 11. Only data for those months in which a complete series of plankton samples were obtained from all the six stations are used for this discussion. Larvae of all the species are treated together.

It is clear that all stages were mixed in various proportions in samples from the three depths at each station. Protozoeae were more abundant during peak breeding months.

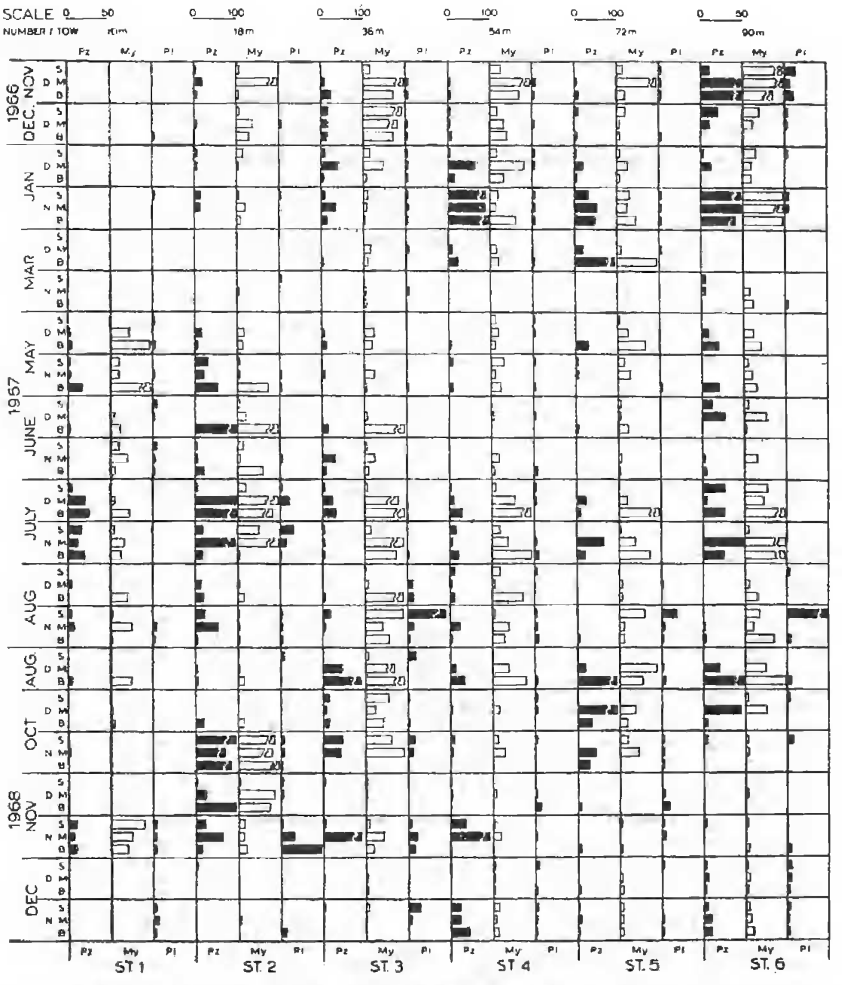

Figure 11. Vertical distribution and diurnal variations of protozoea, mysis and postlarvae at different stations during 1966 to 1968.

Pz	:	Protozoea	(Stipled bars)
My	:	Mysis	(Open bars)
Pl	:	Postlarvae	(Shaded bars)
D	:	Day	
N	:	Night	
S	:	Surface	
M	:	Midwater	
B	:	Bottom	

Though the mid-depths of the six stations are not absolutely comparable, protozoeal and mysis stages showed a general tendency to aggregate at middle levels.

No statistical correlations between different larval stages, and depth, salinity and temperature were found.

Protozoeal stage

Protozoeae appeared by May at 10 m and declined by November. In deeper waters they occurred in most months. From December to March they were taken in deeper waters and increasing numbers were taken with increase in depth.

Vertically, in winter months, more protozoeae congregated at the surface and mid-water at 18 to 36 m. They were more evenly distributed in deeper waters during the day. At night there was a general tendency for larvae to move upward and to be more abundant in surface layers, than in mid-water.

In spring the highest concentration was in the bottom during day and night except at 54 and 90 m, in which depths they were often found in equal abundance at the surface and bottom.

In summer months again they were concentrated on the bottom during the day, and mid-water and bottom at nights in all depths.

In fall, the majority were taken in mid-and bottom levels during day, and surface and mid-levels at night.

Mysis stage

Mysis stages were relatively more abundant than other stages. They appeared in inshore waters by May and became scarce by December. They were taken at all depths in all seasons.

In general, myses showed a tendency to congregate in mid-layers. In winter they were taken more at the surface and mid-water during the day, and mid-water and bottom at night, except at 36 m where they occurred at the surface. On many occasions they were abundant at surface even during the day.

In spring months during the day they were abundant near the bottom except at 36 and 54 m, where they occurred more often in mid-waters. At night they were near the bottom at 10 m, and in mid-layers in other depths.

In summer, they were more abundant at bottom at all stations during the day. At nights they rose to mid-waters and even to the surface at 54 and 72 m.

In fall, except at 10 m they were more abundant in mid-water during day. They were well dispersed at 54 and 72 m depth, and occurred either at the surface, midwater or bottom at other depths.

Postlarval stage

Postlarvae were taken in small numbers in all depths in all seasons. In general, they occurred more at Stations I to III in winter months. They were more randomly distributed in vertical depths at each station than the other two stages. Occasionally they were taken in greater numbers in surface plankton as in November 1967 (St. VI, day), July 1967 (St. II, night), August 1967 (St. III & VI, night); in midwaters as in July 1967 (St. II, day); or in bottom plankton as in November 1968 (St. II, night). No definite seasonal trends were observed in vertical distribution. Probably their power of motility bestows on them more freedom of movement compared to earlier stages.

From the foregoing it is evident that vertical distribution of protozoeal and mysis stages differs with respect to seasons, depths and day and night. At no time was there a definite stratification according to stage, i.e., protozoeae at the bottom, myses in midwater and postlarvae at surface, exclusively. All stages occurred mixed in the meroplankton with varying proportions. In general, depth distributions of protozoeal and mysis stages follow similar trends, which emphasizes the fact that these two stages stay together. Unfortunately, not enough nauplii were collected for a discussion of their vertical distribution.

Diurnal variations

The data indicate that night stratification of larvae was not, as a rule, opposite to that during day. On several occasions protozoea and mysis stages were concentrated at the surface during the day, and in bottom plankton at nights. On other occasions both stages were abundant in midwater during both day and night. In general, larvae appeared to be evenly distributed vertically at nights, and to show abundance at a particular depth during day (Fig. 11).

DISCUSSION

HYDROGRAPHY

The salinity gradients through depths from 10 to 90 m follow the expected trends with increasing values seaward, and at each station the increasing gradient is from surface to bottom. The fluctuations at each station are complicated by rainfall, land runoff, Mississippi River discharge and currents. How far these seasonal fluctuations affect the breeding seasons is not certain.

Temperature patterns described are typical for any open sea environment. While the surface is subjected to heating by solar radiation, subsurface temperatures are influenced by cur-

rents and advection. The trends of temperature variations shown here agree with those described by Drennan (1968). The minimum and maximum temperatures for any locality are of paramount importance to the breeding activity of marine animals as has been demonstrated by Thorson (1946).

In general, the Gulf of Mexico is unique as far as hydrography is concerned. The existence of semi-permanent rotary circulations in the central Gulf and its effects on northern and eastern waters have been shown by Drummond and Austin (1958), Armstrong and Grady (1967) and Armstrong, Grady and Stevenson (1967). The Mississippi River starts discharging great amounts of fresh cold waters in March of each year (over 10,000 m^3/sec), and subsides by May or June. Therefore, it is not unusual to find pockets of low salinity waters in March, May and June. It is also evident that the spring discharge influences the temperature profiles at Stations III to V (Fig. 2). The other factors that bring about hydrographical changes in the Gulf of Mexico in general, and the northeastern Gulf in particular, are subtropical underwater currents, the loop current from Yucatan channel through the Florida straits, upwelling in winter, westerly currents from Mobile Bay, and the outflow from Mississippi Sound, and the mixing of different kinds of waters which has been demonstrated by Drennan (1968). Further, surface divergence brings to surface high-salinity, cool waters, and convergence introduces low-salinity, warm waters (Drennan 1968). In view of these factors it is not possible to explain the fluctuations of temperature and salinity off the Mississippi coast in terms of regular patterns.

SEASONAL AND HORIZONTAL DISTRIBUTION

Among the several methods that are employed to study the reproductive cycles of marine invertebrates a study of the larval abundance yields fairly reliable information. This method has been adopted by several workers on molluscs and other invertabrates as reviewed by Korringa (1957) and Giese (1959), and on penaeid shrimp by Eldred *et al.* (1965) and Temple and Fischer (1967). The spawning periods and areas have also been delineated by studying the mature adults (Kutkuhn 1962). Both these methods have certain merits and shortcomings. Ripeness of the gonads indicates imminent spawning though unfavorable conditions may set back the process of gamete release. Thorson (1946) has shown that critical temperatures for maturation and spawning are different for many Danish bottom invertebrates. If the temperature is not right, ripe ova may be resorbed as has been shown in oysters by Loosanoff (1969). The spawners may survive the adverse environment and successfully spawn on the return of favorable ambient factors (Loosanoff and Davis 1963). Therefore, conclusions mainly based on the occurrence of mature adults, without taking into

consideration the critical temperature requirements, should be made with caution.

The development of embryos and larvae are also dependent on critical temperature requirements. Cook and Murphy (1965b) have shown that no brown shrimp larvae underwent complete development below 24 C; that naupli did not survive the molt to protozoea I at 18 C and that growth was faster between 27 and 30 C. They obtained the first postlarva after 11 days at 30 C, 12 days at 27 C and 15 days at 24 C. But postlarvae start growing at a temperature between 11 and 18 C, and show maximal growth rate in the temperature range of 17.5 to 25 C (Zein-Eldin and Aldrich 1965, and Zein-Eldin and Griffith 1966). It is not known whether the optimum temperature for growth of larvae and postlarvae is significantly different. Mukhacheva (1959) has shown that eggs of *Eleginus gracilis* (Gadidae) develop only when the temperature is –2.8 to 8C; and eggs of *Crassostrea virginica* do not develop if the water temperature is below 15 C (Loosanoff and Davis 1963). There are certain unproved indications that eggs or larvae of several common marine invertebrates on the Gulf coast may overwinter and suddenly effloresce in the spring. It is possible that spawning may occur at 17 C but the eggs and the larvae may not undergo complete metamorphosis until the temperature rises above 24 C. On the contrary, they may metamorphose at 17 C if the larvae need the same temperature as the postlarvae for maximal growth. However, the occurrence of protozocae, myses and postlarvae at deep stations even in winter (bottom temperature above 18 C) is interesting. Possibly these larval stages may not grow in winter, but their presence in a water column may indicate previous spawning. With these reservations it is assumed here that spawning occurs in the temperature range of 17 to 29 C. The larvae may take longer time to grow to postlarval stages in the cooler season because the length of pelagic life depends on the ambient temperature (Cf. Thorson 1961). The purpose of the present investigation is to understand the spawning seasons, and does not focus on growth factors of the larvae. The spawning seasons are discussed here with these reservations in mind.

Besides the temperature as a factor, penaeid larvae are subjected to the same ambient factors that affect plankton in general. During the present investigation, as a working hypothesis to interpret seasonal larval pluses at different depths, areas of larval concentration were assumed to represent breeding localities. The movements of the spawners are assumed to be indicated by the occurrence of larval aggregations at different stations. The conclusions based on the larval pulses need not necessarily give an accurate idea of the incidents in the open sea environment in view of the arguments presented hereunder, for and against such a hypothesis.

Some factors that influence the larval distribution are the movements of the organisms themselves, predation, adaptibility of the larvae to the environment, transport by currents, and illumination. Thus, nauplii, protozoeae and myses are capable only of feeble movements with the aid of the first antennae (Ewald 1965) and they may not by their own motility travel great distances. Further, penaeid larvae belong to the category or organisms with relatively short pelagic life, (10 to 12 days), and a great stability of occurrence characterizes such larvae (Thorson 1946). Finally, several fish, *Sagitta*, and medusae have been observed to feed on penaeid larvae, and this predation may cause scarcity.

Currents are of great importance for the transport of pelagic animals, and in some cases for survival (Davis 1955). Tidal currents particularly influence organisms in inshore waters less than 15 m deep. Many animals adapt their physiological rhythms to such tidal currents with the results they are transported landward during flood tide as in *Lucifer* (Woodmansee 1966). Thus, tidal currents may transport penaeid larvae from 10 m deep waters into coastal bays. Idyll *et al.* (1962) have shown that currents off the Florida coast are tidal in waters less than 15 m deep, tidal and wind driven at 15 to 33 m depths and density related in deeper waters. Generally spawning grounds are located where strong tides do not exist. Further, it is also possible that shrimp prefer suitable areas for spawning so that larvae will not be exposed to adverse water currents. Johnson (1939) has shown that *Emerita* breed in such favorable areas in relation to currents. Surface currents, essentially wind-produced, may carry the larvae along the flow. On the other hand, subsurface currents are density effected. Heavier organisms such as nauplii, protozoeae, myses, and even eggs are unlikely to be carried away by these currents. These larvae show a tendency to stay in a water column, performing only weak vertical movements. Postlarvae, which can swim forward, are the exception (Ewald 1965). Therefore, sampling at three levels, as has been done in the present study, will compensate for such pelagic transport and may give reliable information on abundance.

Thorson (1946) has shown that a) occurence of swarms in a particular area to the exclusion of adjacent localities would indicate massive current transport, and b) occurence of older and younger larvae in different regions indicates current transport. The average fair representation of penaeid larvae in the samples precludes current transport of significant magnitude. Though larval pulses are noticed at certain depths, larvae still occur at other depths. Finally, younger and older stages invariably can be collected from any station and any depth. This appears to be a rule for crustacean larvae in general (Gurney 1924, Pearson 1939, Eldred *et al.* 1965, Temple and Fischer 1965 and 1967). Based on such mixed collections, Gurney con-

cluded that crustacean larvae may not be at the mercy of currents as much as is supposed, and Pearson agreed with him. Though currents influence the distribution of the larvae, larval studies can provide a good idea of spawning activity and locations for penaeid shrimp, in view of the arguments presented here.

Finally, eddies of gyrating currents (non-tidal) are believed to be effective in supporting a self-sustaining population of specific planktonic forms (Sverdrup, Johnson and Flemming 1946, Davis 1955). Where such eddies exist, plankters may not drift too far away from such gyrations but may be circulating in a specific area. That such eddies exist off the Mississippi coast has been shown by Drennan (1968) and Armstrong *et al.* (1967). Therefore, it is possible that penaeid larvae stay in a particular area in the offshore waters for some time after the spawning of the adults. However, postlarvae can swim landward and can make use of tidal currents to gain entry into coastal bays, with the aid of their endogenous tidal activity rhythms (Hughes 1967a).

Both the methods of determining spawning seasons and loci have weak points. While adults can move on their own, subject to circadian and feeding rhythms (Hughes 1967b), larvae are exposed mainly to natural mortality, predation, and current transport. Nevertheless, sampling at three levels and at different depths will yield reliable information on the spawning activity. During the present investigation a good correspondence was found between the seasons of occurrence of mature adults of *Penaeus, Trachypeneus* and *Sicyonia* species and of their larvae. Thus, spawning seasons can be delineated based on both factors. However, demarcation of spawning loci based on a single factor may not be accurate. It is likely that a more accurate picture of spawning areas can be based on the occurrence of eggs and larvae if the reservations presented above are borne in mind. Finally, study of the adult or larval concentrations at a specific depth will not yield correct information on the spawning seasons in view of the temperature control of breeding, and of the movements of adults along the increasing temperature gradient.

General

It has been shown that spawning is pronounced when temperature rises above 17 C. At 10- and 18-m stations, rise of temperature to above 20 C in May, and fall from above 25 C to 20 C in September induce intense spawning activity. As temperature drops in shallow waters shrimps follow a temperature gradient and spawn in deeper waters in winter. Year round breeding is evident if various depths are considered. Orton (1920) states that marine animals are stimulated to breed

either by a specific temperature (physiological constant) or by a rising or falling of temperatures in a particular area. The present findings agree with this rule. Thorson (1946) emphasized that minimum and maximum temperatures are critical for breeding. In the case of shrimps in the Gulf of Mexico the minimum temperature is 17 C and maximum 29 C. Gunter (1957) states, with reference to shallow water species, that all shrimps are spring or summer spawners. Taking the group as a whole, present findings and those of Temple and Fischer (1967) indicate that penaeid shrimps, including deep water species, breed throughout the year in areas where temperature remains within a range of 17 to 29 C. A protracted spawning season, based on larval abundance, has also been reported for *Penaeus duorarum* off the Florida coast (Roessler *et al.* 1967). The European oyster starts spawning when temperature rises above 15 C and continues the activity as long as temperature remains above 15 to 16 C (Orton 1920, Korringa 1957). The environment for the shrimp in the Gulf of Mexico appears to lead to an analogous situation.

These findings point out that penaeid shrimp have protracted spawning seasons. This may be due to a) great vertical distribution of the species, b) different timings of gamete release by younger and older males and females, c) several spawnings of individual females in a season. An extended season implies asynchronous spawning, that is some shrimp are in early stages of maturation, some are getting ready to spawn, some are spawning and others are spent (Giese 1959). Adults caught in the trawls during the present study were in various stages of maturity in any month. Secondly, females of *Penaeus fluviatilis* are known to spawn up to four times a season (Lindner and Cook 1967). Postlarvae migrate into estuaries in two or three waves in summer (Gunter 1950, Lindner and Anderson 1956). After each spawning female gonads rejuvenate and produce more batches of eggs as has been shown for *P. fluviatilis* (King 1948), *P. indicus* (Subrahmanyam 1965b) and four other penaeids (Rao 1968). Lastly, many species have a wide range of distribution (Burkenroad 1934), and younger and older spawners invariably occur mixed in any area. These observations indicate that penaeid shrimp can spawn over a long period of time.

Though the breeding season is protracted, distinct pulses of larvae are observed in spring, summer, fall and winter, depending on the depth of the water column. Mainly there appear to be summer and fall peaks. Periodicity in breeding is a general phenomenon even under stenothermal conditions such as tropical environments, as has been shown for the brackish water fauna of Madras (Panikkar and Aiyar 1939), Great Barrier Reef invertebrates (Stephenson 1934) and *P. indicus* (Subrahmanyam 1963).

It is significant that during spring and summer the spawning center is at the 18-m station. This has survival value for the species because postlarvae have easier access to the estuaries. From 10 to 12 days are required for the nauplius to become a postlarva at 25.6 C (Johnson and Fielding 1956). In colder months this may take longer because temperature controls the length of pelagic larval life (Cf. Thorson 1961). Thus, when the spawning center shifts to deeper waters in colder months the postlarvae still have a chance, if growth is retarded, to enter the coastal bays on the return of warm temperatures. They may overwinter offshore and enter the bays in spring as it has been suggested for brown shrimp along Texas coast (Temple and Fischer 1967).

Abundance in relation to depth

The data indicate that unimodal spawning occurs in waters up to 18 m deep and bimodal activity in deeper waters. The peaks are observed progressively later in the year as depth increases. In *Penaeus* the summer peak shifts from 10 m in July to 36 and 54 m in August; the fall peak shifts from 10 m during September to 18 and 36 m during October; and to 54 and 72 m in November. A January peak is seen at the 90-m stations. These indicate movements of spawners. Similarly in *Trachypeneus* the fall peak shifts from 10 m during September to 36 and 54 m during October and November. *Sicyonia* shows identical trends. *Parapenaeus* and *Solenocera*, however, do not show such distinct shifts of peaks.

Temple and Fischer (1967) also demonstrated such trends in the shifts of larval maxima. They showed that spawning occurs even in December at 46-m depth, and that the breeding season is more protracted in deeper water compared to the May to October period at 14 m. Eldred *et al.* (1965) have shown that the intense spawning season commenced a month or two later at 10-25-m depths compared to the season in 3-9 m for Trachypeneus and *Sicyonia*. Since these authors did not study deeper waters they could not demonstrate year round spawning in depths greater than 36 m, which is a significant point found in the present study. The same authors came to the conclusion that the minimum spawning temperature for *Penaeus duorarum* is 23.9 C, but they later collected larvae at 25-to-36-m depths when the temperature was 19.2 C. It is clear, therefore, that spawning occurs in the temperature range of 17 to 29 C and the spawners move along with the increasing temperature gradient with depth.

The spawning seasons delineated by various authors for different species are in agreement with the present findings. Most of the authors, however, studied a particular depth and the occurrence of mature adults there. When the larval abun-

dance is studied, taking into consideration a wide range of depths, year round spawning activity becomes apparent. Spawning may start early in deeper waters and last longer, while in shallow waters it starts later and ends earlier.

Spawning loci of the species

The spawning areas of the different species of the six genera show a good correlation to the bathymetric ranges given by Burkenroad (1934) and Williams (1965). The species with a wide bathymetric range breed as close to the shore as possible during warm seasons and offshore during cooler months. It is interesting that *Parapenaeus and Solenocera* spawn at 18-to-36-m depths in the cooler season and at 54-to-90-m depths during summer. When shallow water species are spawning in the area of their depth range, species of these two deep water genera have moved out to deeper waters. In the cooler season, when the shallow water species move offshore, the deep water species move into shallower waters.

It has been shown that though the species spawn in their entire range of distribution they prefer certain depths in specific seasons. Eldred *et al.* (1965) were also able to observe such shifts in the spawning loci. They showed that *P. duorarum* spawned intensely either in 3 to 9 m or in 25 to 38 m; *Trachypeneus* in 3 to 9 m; *Sicyonia* species in 3 to 38 m with distinct seasonal pulses at specific depths; and *Parapenaeus* chiefly beyond 25 m. Ingle *et al.* (1959) pointed out that large females offshore may have less rigid temperature requirements for spawning, but it is more likely that penaeids can spawn year round in deep waters because of small scale offshore temperature fluctuations.

Thus, larval maxima indicate spawning loci of the species, and definite seasonal trends in the occurrence of peaks at specific depths argue against effective current transport. Pressure changes at certain depths may also regulate the release of larvae or embryos as has been shown for *Spirorbis borealis* (Knight-Jones and Morgan 1966). Therefore, it is possible that the maximum number of eggs may be liberated by females at favorable depths. The larvae, in view of their power of keeping together (Gurney 1924), may not drift too far away from such area until they become postlarvae. Although the larval pulses shed light on the movements of the spawning population. adults may not be captured during larval peak abundance.

Larval abundance in relation to occurrence of adults

No correlations were found between adult numbers and larval abundance. This would mean either that the adults moved away from the area of spawning, or that the larvae

were carried to the sampling areas by currents from some other areas. However, the ecological requirements of adults and larvae are not identical, and spent females may have different needs. It is significant that several times adults, but not larvae, were captured in specific areas. *Penaeus plebejus* and *P. esculentus* do not necessarily spawn in their areas of concentration (Racek 1955). It is more likely that adults can move far and wide with the benefit of their activity controlled by a circadian and a 24-hour feeding rhythm (Hughes 1967b), while larvae have feeble motility. Further, adults were not taken at the 10- and 18-m stations where thousands of eggs were collected (Figs. 3 and 4). Thus, here is additional evidence that determination of spawning loci based on the adults does not always yield the correct picture.

POSTLARVAL ABUNDANCE IN RELATION TO LARVAL OCCURRENCE

Following every larval peak a postlarval peak, either white shrimp or brown shrimp, is noticed in the open sea. White shrimp postlarvae are abundant in March, May, June, July and September, and intense spawning occurs at 18-m depth during these months. Christmas *et al.* (1966) have shown that white shrimp postlarvae start appearing in Mississippi Sound in May, reach a peak in June, July or August and decline by October. Thus, there is good correlation between the two trends. The Sound postlarvae come from broods in the open sea.

Postlarvae of brown shrimp first appear in the inside waters in February, and reach a peak in April, June and August. The abundance in the open sea bears a positive relationship to that in the Sound. However, fair numbers of postlarvae occur in December and January. Since brown shrimps appear to breed in deep waters during this period, it is likely that these larvae overwinter offshore and move into the estuaries in February or March. Temple and Fischer (1967) came to a similar conclusion in view of the slightly larger size of the postlarvae during the January to April period. Further, postlarvae bury themselves in mud at temperatures lower than 17 C and become active only at higher temperatures (Aldrich *et al.* 1968).

It may be possible to predict the shrimp fishery in Mississippi Sound based on a larval index in the open sea. Following a spawning success, postlarvae can be expected to enter the Sound within three or four weeks. The average annual production of pink shrimp protozoea in South Florida has been estimated to be 87.0×10^{11}; the survival rate was 74 to 98% per day; 0.05 to 0.14% of the original protozoeal population survived to become postlarvae; and 6% of the postlarvae survived to produce the commercial catch of 5×10^{8} individuals in

1963 (Roessler *et al.* 1967). Such calculations can be based on the larval numbers obtained by sophisticated sampling. Also, from a long range study it is possible to predict the recruitment seasons for the postlarvae in the estuaries as has been shown by Williams (1969) in North Carolina waters. Because of their fast growth rate, a millimeter or more per day in summer (Viosca 1920, Gunter 1950, and Williams 1955), postlarvae can reach commercial size in three months. Therefore, a larval peak in open sea should be followed by maximal commercial catches in four or five months, allowing a wide margin for the hazards of dispersal, mortality, predation, unfavorable temperature and other ambient factors that affect larvae in the open sea and postlarvae in the coastal bays. It also appears that from the time of hatching about six or seven months are required for the subadults to return to the sea to become mature adults. This surmise is in agreement with the earlier findings of various authors. An uncertain correspondence between postlarval abundance and commercial catches has been shown (Christmas *et al.* 1966). On the other hand, Williams (1969) has shown that no correlation existed between the two factors off North Carolina during a period of 10 years. As the evidence is not conclusive, it will be interesting to examine the relationship between larval, postlarval and commercial catch indices.

VERTICAL DISTRIBUTION

No chronological abundance of stages in vertical depths can be demonstrated, and concentrations of protozoeal and mysis stages can be expected at any level in any season in any depth. Protozoeae and myses have more or less similar, though not identical, patterns of distribution. Postlarvae seem to be distributed at random in vertical depths in all seasons. Larvae of marine invertebrates in general are known to be positively phototactic. The organisms become negatively phototactic as they grow older (Thorson 1946). It is probable that both protozoeal and mysis stages may assemble at levels where optimum light occurs. It is not understood why they do not migrate to surface, as a rule, at night.

Temple and Fischer (1965) state, based on collections from four cruises, that during June, July and September protozoeal and mysis stages occur more abundantly near the bottom, while in November they are more evenly distributed vertically. The present, more extensive data indicate that no such definite patterns occur in the summer and early fall months. Even in fall, greater concentrations can be found in bottom layers. Further, during winter both stages were taken in maximal abundance at the surface, even during the day.

Vertical distribution of planktonic animals, including meroplankters, is controlled by several factors, such as direction and speed of movement of species (Szlaeur 1963), hydrostatic pres-

sure (Hardy & Bainbridge 1951, Knight-Jones and Quasim 1955), and salinity, oxygen, dissolved nutrients, viscosity and density (Russell 1927). It has been shown that animals in the upper part of a population respond more to light, and those in bottom layers more to temperature. The depth at which any group occurs reflects isolume movements in the upper part and isotherm movements in the lower part of the population. Also, random movements about an optimal depth result in vertical spread (Moore 1956). Light is believed to be a major factor in distribution (Cushing 1951). Further, four major types of responses in relation to hydrostatic pressure are known to occur in planktonic animals with respect to vertical distribution, namely (1) orientation to gravity alone, (2) orientation to gravity with the subsidiary effect of light, (3) orientation to light alone and (4) no response to pressure changes. Increased pressure induces positive phototaxis, and decreased pressure, passive sinking (Knight-Jones and Morgan 1966). Larvae can also avoid depth changes by endogenous reversals of phototaxis. Responses to pressure changes also depend upon the physiological state of the species (Knight-Jones and Morgan 1966). Temperature changes also influence vertical distribution. Warming and cooling of water may influence heliotropism, altering it from negative geotropism to positive geotropism; and temperature rise may bring about negative phototropism and *vice versa* (Russell 1927).

During the present study only temperature and salinity were considered, and since so many factors are involved in regulating vertical spread of larvae, it is difficult to explain the patterns of vertical seasonal distribution of protozoeal, mysis and post-larval stages. However, isothermal conditions during winter and fall combined with less illumination at the surface may explain the wider vertical spread of the stages during these periods, even during the day. In summer the larvae are seen to be more restricted to bottom layers during day and to bottom and midwater at night. Sometimes larvae were absent in the surface waters (Fig. 11), possibly because of more illumination of top layers and negative phototropism induced by temperature rise.

Crustacea, including planktonic larvae, are known to perform diurnal migrations (Russell 1925 and 1928). An excellent review on the subject is given by Bainbridge (1961). The mechanisms for these migrations appear to be active swimming, vertical currents, viscosity of water layers and temperature changes. Several factors such as light, gravity, pressure, temperature and phytoplankton are believed to affect vertical diurnal migrations. The combined effects of light, temperature and pressure changes in a day cycle appear to be the more important (Moore 1955, 1956).

Although a 24-hr study was not made during the present investigation, there are indications that larvae have a tendency to rise toward the surface at night, or that they are evenly distributed in the vertical column. Second and third protozoeae and myses have been reported to undertake considerable vertical movements; they may aggregate at a depth or spread out depending on optimum conditions. It has not been demonstrated that, as a rule, planktonic shrimp larvae congregate in the surface layers during night. However, they may be scarce at the surface from midnight to midday, and may rise to surface layers from midday until the following midnight (Roessler *et al.* 1967). Temple and Fischer (1965) claim that such larvae show a distinct ascent to surface at night. However, their data do not lend themselves to such broad postulations. Postlarvae appear to behave more in a classic diurnal rhythm of ascent and descent, though not always. The present data indicate that protozoeal and mysis stages do not congregate, as a rule, in surface layers with the advent of night. Random patterns of distributions are more prominent. Since information on the behavior of penaeid larvae is lacking, interpretation of the diurnal patterns of vertical distributions through seasons is not possible.

It is concluded, therefore, that protozoea and mysis stages show random patterns of vertical distribution; show a tendency to be in midwater layers; congregate near the bottom during summer months; show a tendency to rise to the surface in winter months; and show no stratification in a water column in relation to the ontogenic stage. Postlarvae are randomly distributed. Though typical diurnal migrations to surface from bottom and back are not observed, there is a general tendency on the part of the larvae to rise toward surface layers or to become more evenly distributed vertically, in response to decreasing light.

SUMMARY AND CONCLUSIONS

1. An investigation was carried out from November 1966 through December 1968, on the relative abundance and seasonal and spatial distribution of penaeid shrimp larvae off the Mississippi coast of the Gulf of Mexico.

2. Six stations were established between 29°N and 30°N latitude, and between 88°12′W and 88°47′W longitude. The depths of the stations were: St. I, 10.7 m; St. II, 18.3 m; St. III, 36.6 m; St. IV, 54.9 m; St. V, 73.1 m and St. VI, 91.5 m.

3. Plankton collections were made with a No. 3 Nylon closing net, that had mesh size of 0.33 mm, length of 2 m and diameter of 50 cm across the mouth. Three simultaneous

tows of 20 min duration were made at surface, midwater and bottom levels at each station. Attempts were made to obtain a complete series of day and night collections every month.

4. Penaeid larvae were separated from the rest of the plankton and identified to stage and genus. They were preserved in 5% buffered formalin (with borax and glycerine). Larvae studied represented six genera, namely *Penaeus*, *Parapenaeus*, *Trachypeneus*, *Xiphopeneus*, *Solenocera* and *Sicyonia*.

5. Trends and patterns of salinity and temperature of the area are described and discussed. The fluctuations of these two factors are brought about by Mississippi River discharge, eddy systems and other kinds of water movements and mixing. While bottom temperatures fell to 12 C in the inshore waters in winter they remained uniformly above 16 C in 54 to 90 m throughout the study period. Isothermal conditions existed in winter and fall, while some mixing was evident in spring. In summer, thermal stratification was evident only in 10 to 18 m.

6. Temperature changes were more marked at the 10-m station and less marked at the 72- and 80-m stations. The range of variation was 17.8 C, between 12.3 and 30.1 C, at Station I, and diminished to 9.4 C, between 17.4 and 26.8 C, at Station VI. Surface temperatures fluctuated with a greater range than mid-water and bottom temperatures. The range was 12.2 to 30.4 C, 12.2 to 31.0 C, and 12.5 to 29.5 C at surface, midwater and bottom, respectively, at Station I; and 17.8 to 30.4 C, 17.2 to 28.0 C and 17.2 to 21.9 C respectively at the three levels at Station VI. Bottom temperature varied from 12.5 to 26.1 C in 10-m depth, the range decreasing gradually with increasing station depth. The variation was between 16.7 and 20.0 C in 90-m depth.

7. Salinity fluctuated from 18.5 to 36.6‰ in 10-m depth and the range decreased at deeper stations, the variation being between 26.8 and 38.0‰ at the 90-m station. Surface salinity varied more than mid-water and bottom salinities at all the stations. The ranges for the surface, mid-water and bottom at Station I respectively were 13.1 to 37.1‰, 19.0 to 37.6‰ and 19.9 to 37.6‰, and for the three levels at Station VI were 23.2 to 38.0‰, 23.3 to 38.0‰ and 26.6 to 38.0‰.

8. Determinations of spawning seasons and areas were made by considering the abundance of eggs and of nauplius, protozoeal and mysis stages of the species of the six genera.

9. No correlation was found between the occurrence of mature adults of *Penaeus* spp., *Trachypeneus* spp. and *Sicyonia* spp. and of their larvae in a particular area. Adults were taken in some depths where larvae were scarce and *vice versa*.

10. In general, spawning of all species of the six genera seemed to occur within the bottom temperature range of 17 and 29 C. Intense spawning was associated with rising temperatures in spring and falling temperatures in late fall or winter. As long as the temperature remained above 17 C spawning activity prevailed. A unimodal pattern of spawning was observed at 10- and 18-m stations; and a bimodal pattern at 36-, 54-, 72- and 90-m stations.

11. The spawning season of penaeids studied was protracted with distinct pulses in spring, summer, fall and winter. During spring larval concentrations were observed at the 18-m station, during summer at 18-to-36-m stations, during fall at 18-to-54-m stations and during winter at 54- to 90-m stations. This indicates that species breed close to shore during warmer months, and move away from inshore waters as temperature starts falling.

12. Species of *Penaeus, Trachypeneus, Xiphopeneus* and *Sicyonia* spawned mainly from April to November, and even in winter in waters deeper than 54 m. Species of *Parapenaeus* and *Solenocera* bred intensely during fall, winter and spring. While shallow water species spawned in all depths of their bathymetric range during warmer months, deep water species like *Parapenaeus* and *Solenocera* spawned in deeper waters. During the cooler season shallow water species moved offshore and deep water species moved into waters less than 54 m deep. Then there appeared to be some overlapping between the inshore and offshore species as far as the breeding areas were concerned.

13. *Penaeus* larvae occurred in all depths, *Trachypeneus* mainly between 10 and 36 m, *Solenocera* beyond 18 m, *Sicyonia* in all depths, and *Parapenaeus* mainly beyond 18 m. The larval distribution showed a relationship to the bathymetric distribution of the adults.

14. When maximal numbers of larvae were considered, definite inshore and offshore movements within the bathymetric range of species, were obvious. *Penaeus* spp. spawned in all depths, mainly at 18 m in summer, 36 m in fall and 72 to 90 m in winter. These larval maxima could belong to white and pink shrimp in shallow waters, and to brown shrimp in deep waters. *Trachypeneus* spp. mainly spawned at 18 to 36 m, *Xiphopeneus* at 10 to 72 m, *Parapenaeus* at

56 to 90 m, *Sicyonia* at 18 to 54 m, and *Solenocera* at 18 to 54 m. Larval maxima, thus, give some indication of spawning loci of species.

15. The relationship between spawning success and postlarval abundance of white and brown shrimp was examined. During the main spawning season increase and decrease in larval numbers in alternate months was noticed. For every corresponding valley in the larval abundance curve there was a postlarval peak, either of *Penaeus fluviatilis* or *P. aztecus*. The patterns of occurrence of postlarvae of these two species in the open sea agreed with those observed in Mississippi Sound during a study made previously in the area. Though it is not possible to distinguish the larvae of the three species of *Penaeus*, some understanding of spawning activity of each species can be derived from postlarval abundance.

16. The vertical distribution of protozoeal, mysis and postlarval stages of all the genera has been studied. Protozoeal and mysis stages showed similar patterns in their vertical spread. During the spring and summer months they were more restricted to sub-surface layers during day, and occurred in upper layers at night. In winter months they were found in large numbers in surface layers even during day. In general, they showed a tendency to aggregate in mid-water layers and sometimes at the surface. Postlarvae showed random patterns of vertical distribution. Temperature, light and pressure appeared to be the main factors controlling depth distribution.

17. A stratification of larvae in vertical profile in relation to ontogenic chronology was not found. Even when there was no vertical mixing of water protozoeae occurred in surface layers, and postlarvae could be found in good numbers near bottom. Eggs were found mainly either near the bottom or in mid-waters.

18. The classic pattern of diel migrations was not shown either by protozoeal or mysis stages. In general, they showed a tendency to ascend to upper layers during night or to spread out evenly. Even during daylight hours they could be found at surface, and at night near the bottom. Postlarval distribution in the vertical column was random with respect to the diel cycle.

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